FLOWERING PLANTS

AND

FERNS.

VOLUME I

A MANUAL AND DICTIONARY

OF THE

FLOWERING PLANTS

AND

FERNS

BY

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VOLUME I.

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PREFACE.

THE aim with which I commenced, nearly seven years
ago, to prepare this book, was to supply within a
reasonable compass, a summary of useful and scientific
information about the plants met with in a botanical garden
or museum, or in the field. The student, when placed
before the bewildering variety of forms in such a collection
as that at Kew, does not know where to begin or what to
do to acquire information about the plants. The available
works of general reference are mostly very bulky and often
out of date, and as a rule refer only to systematic or
economic botany, and say nothing about morphology or
natural history. I have endeavoured to bring together in
this book as much information as is required by any but
specialists, upon all plants usually met with, and upon all
those points—morphology, classification, natural history,
economic botany, &c.—which do not require the use of a
microscope. The study of the external features of plants
is in danger of being too much overshadowed by that of
the internal features; this is largely due to the excellent
organisation of our laboratories for teaching anatomy and
physiology, and to the fact that the teaching of systematic
botany upon modern lines, in connection with the subjects
of evolution, morphology, natural history and geographical
distribution, is as yet in its infancy. I have found in my

own experience that it is possible by combining the treat-
ment of these subjects to rouse an interest in even the
details of classification. It is admitted on all hands that
there is a great dearth of young systematists, and that there
never was greater need of them than now, when civilisation
is rapidly destroying the primeval vegetation in all quarters
of the globe; this is perhaps the effect of the causes men-
tioned above, and it is my hope that this book may do a
little towards removing one of them.

The principal part of the book consists of a dictionary
in which the whole of the families and the important genera
of flowering plants and ferns are dealt with. The families
are treated very fully, more so than in any ordinary text-
book of systematic botany, whereas the genera are treated
much more briefly unless they show some feature of special
interest that is not common to the family. This mode of
treatment has been adopted for two reasons—to prevent
the student from regarding the genera as isolated and un-
connected units, and to avoid repetition. To give the
generic characters in a work of this kind would obviously
be of little or no practical value, and would enormously
increase the bulk. The treatment adopted involves a good
deal of cross-reference, but will impress upon the student
the relationships of the members of the vegetable kingdom
to one another. Again, some who have examined the book
in course of writing have complained of the absence of
directions as to where the plants may be found. In a
book for general use it is impossible to supply such direc-
tions, and an introductory chapter upon botanical gardens
in general has therefore been inserted, after reading which
there should be no great difficulty in finding any plant
required, for the dictionary gives information about the
climate from which it comes. Another fault in the book,
and a more serious one, is the absence of all but a few

figures. This also is rendered necessary by the limitations of the space at command. Floral diagrams of most of the largest families have been inserted, and also some illustrating those groups whose morphology is difficult, *e.g.* the Marantaceae.

Finding that Part II was still wanting in co-ordination, I wrote Part I to supplement it. At first this was intended only to be a kind of index to Part II, as the chapter upon economic botany still is, but it was soon found necessary to enlarge upon this and to write what is practically a text-book of morphology, classification, natural history and geographical distribution. Our existing text-books of morphology are mostly out of date and have little evolutionary basis; the principles of classification and evolution are not explained in the elementary books, and the advanced books take for granted that the reader is familiar with them; no good text-book of the natural history of plants or of their geographical distribution is at present available in English. I have therefore written Part I in such form that it makes in itself a fairly complete treatise upon these subjects; at the same time it is throughout designed for purposes of cross-reference from Part II, and may be itself expanded to almost any extent by reference to Part II for details. The method of treatment adopted is novel, and is based on that which I have employed for several years in my lectures. The morphology of the vegetative organs is dealt with generally in Chapter I, and in more detail in Chapter III in connection with the natural history and geographical distribution (Chapter III resembles Professor Warming's *Plantesamfund* in its mode of treatment, but was written before I had seen that work, from which however I have borrowed a few suggestions); the morphology of the flower is treated in full in Chapter I, in connection with its natural history and from an evolutionary standpoint. I

have adopted this method both because it seems to me to make more clear the meaning of morphological phenomena and the connection between morphology and other branches of botany, and because I have wished to place before the student some of the general ideas underlying modern re-search, with a view to suggesting directions in which further research is desirable and likely to be profitable.

The second portion of this work is of course chiefly a compilation; a few original observations are inserted, but none of any importance. I desire in the first place to express my warmest thanks to Professor A. Engler, for his kind permission to use the materials contained in *Die natür-lichen Pflanzenfamilien*, a permission of which I have very largely availed myself, the descriptions of many of the families being almost entirely based upon that work. I am also indebted to him and to Herr Engelmann for the use of the late Professor Eichler's figures. Many other books, and hundreds of original papers have also been used in pre-paring Part II; the chief of these are mentioned on a later page.

The article referring to Kew Gardens has had the ad-vantage of revision by Mr W. T. Thiselton Dyer; Professor Bower has read all the parts relating to the Pteridophytes, as well as Chapter I; Professor Marshall Ward has revised the proofs of Part II; Miss M. Baldwin has prepared the Index; Mr I. H. Burkill has revised for me all the last part of the book and corrected the proofs. To the kindness of all these friends I am deeply indebted. For kindly en-couragement and many suggestions I have to thank Mr F. Darwin, to whose teaching I largely owe whatever is of value in the mode of presentation of the facts. I have also to express my obligations to Mr A. C. Seward, Mr W. H. Lang, Mr A. G. Tansley, Professor Bayley Balfour, Mr A. J. Church, Mr R. I. Lynch, Mr F. W. Moore,

Mr J. Dewar, and many others, for assistance rendered, information supplied, and other services. For placing my time very much at my own disposal during the last two winter sessions I have to thank Professor Bower. Mr A. E. Shipley has assisted me in many ways during the progress of the book through the press and I desire to thank him for his cooperation.

The illustrations are copied from Eichler's figures, partly by myself and partly by Mr Edwin Wilson, to whom I am indebted for their excellence.

Into a work like this, errors must inevitably creep, and I shall be grateful if those who discover them will kindly communicate them to me at the Royal Botanic Gardens, Peradeniya, Ceylon. I shall also be glad to receive suggestions for the improvement of future editions, if such should be called for.

JOHN C. WILLIS.

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Engler: *Syllabus der Vorlesungen.*
Eichler: *Blüthendiagramme.*
Hooker: *Synopsis Filicum.*
Hooker and Jackson: *Index Kewensis.*
Lindley and Moore: *Treasury of Botany.*
von Müller: *Select Extra-tropical Plants.*
Durand: *Index generum Phanerogamarum.*
Just: *Botanischer Jahresbericht,* 1885—1893.

LIST OF ABBREVIATIONS USED IN PART I.

Those used in Part II are given at the beginning of Vol. II those used in Part I are only employed in the Systems of Classification in Chapter II. and in the Introductory chapter.

A, androeceum.	homochlam., homochlamydeous.
alt., alternate.	infl., inflorescence.
C, corolla.	K, calyx
coh., cohort.	loc., loculus, locular.
cpl., carpel.	N. O , natural order.
flr., flower.	opp.. opposite.
G, gynoeceum	P, perianth.
heterochlam , heterochlamydeous	sta., stamen.

☿ , hermaphrodite; ♂ , male, ♀ , female.

⤳, more than; <, less than; ±, more or less; ∞, numerous or indefinite

PART I.

OUTLINES OF THE MORPHOLOGY, NATURAL
HISTORY, CLASSIFICATION, GEOGRAPHI-
CAL DISTRIBUTION AND ECONOMIC USES
OF THE PHANEROGAMS AND FERNS.

INTRODUCTION.

I.

Suggestions to Students as to the method of using this Book.

THE present work is not intended as a mere dictionary of miscellaneous information about plants, but also and in an equal degree as a guide to the scientific study of morphology, natural history, geographical distribution, classification, economic botany &c. A few suggestions, therefore, as to the mode of using the book may not be out of place.

Whilst in Part II. no particular effort has been made to avoid technical language, the most of the terms and expressions employed are so far explained in Part I. that it is hoped the book will be found available by any one who has studied any of the small elementary treatises on Botany (*e.g.* F. Darwin's *Elements of Botany* in this series of Manuals). An explanatory index will be found at the end of the book.

At most schools and colleges the study of Botany is commenced either in April or October. In either case the student will do well to confine his attention during the first summer and autumn to the elements of morphology and natural history; these are dealt with in Chapter I.; specimens should be obtained and dissected and careful sketches made of points of interest &c. The sections in Chapter III. dealing with Herbs, Shrubs, and Trees should also be read. During the winter the student's time is usually occupied with vegetable anatomy, &c., but he should also find time to study carefully the various ways in which plants hibernate and store up reserves for the growth of the next spring; this will naturally lead to a thorough

study of the morphology of buds, tubers, rhizomes and other underground parts.

In February and March a few flowers will begin to appear out-of-doors and the study of classification may be begun. At first no attempt should be made to learn the characters of the natural orders, nor to study the principles of classification, but a thorough study should be made (with the aid of Part II. of this book) of all obtainable plants (and more especially of their reproductive organs) belonging to about a dozen or twenty of the large orders, chosen as representatives of the various sections of the natural system. The following list of orders is a suggestion based on several years' experience in teaching systematic botany:

Compositae, Rubiaceae; Labiatae, Primulaceae, Ericaceae; Umbelliferae, Malvaceae, Leguminosae, Rosaceae, Cruciferae, Ranunculaceae, Caryophyllaceae, Betulaceae.

Orchidaceae, Liliaceae, Gramineae.

Coniferae.

Selaginellaceae; Polypodiaceae.

After a considerable number of plants and flowers of these orders have been examined, dissected and sketched, the student will be able to refer to its relationships any unknown plant of these orders that may be given to him. He will now have a practical acquaintance with the class of facts with which systematic botany deals, and should study the principles of the subject (see Chapter II.) and the different systems of classification in use. He should not however be content with merely finding out the order to which an unknown plant belongs, but should further study the subdivision of these orders into their tribes; this will further help him in grasping the principles of classification. Lastly, with the aid of Hooker's *British Flora* or a similar work he should endeavour to identify the genus and species of all British plants which he recognises as belonging to the orders he has studied. At the same time as he studies the classificatory details of flowers &c., he should of course pay attention to interesting features in their morphology or natural history, and Part II. will aid him in this. The various subjects treated in Chapter III. should also be worked at, taking them one by one and studying them in a

botanic garden or in the field, with the aid of the details given in Part II., and with reference to original papers for further information. A third season may be employed in a similar way by increasing the number of natural orders studied; the new ones will group themselves in the mind round those already familiar. It is best not to attempt to add too many new ones at once to the old; about 50[1] is the most that should be attempted during a season. The subjects of Chapter III. may now be further dealt with and a commencement made upon Geographical Distribution or upon the details of Economic Botany. By this time the student should have a good working knowledge of field botany, and to give further directions here would be superfluous.

II.

BOTANIC GARDENS, ETC.

IN a general work like this, it would be impossible to give details of the positions of the various plants in different gardens, even were they always to be found in the same place. A sketch is given here of the usual arrangement of a botanic garden, with a brief account of the positions of some of the more noteworthy plants, families or types of vegetation in the two gardens most frequently visited by students.

[1] These should at any rate include the following orders: Campanulaceae, Cucurbitaceae, Acanthaceae, Scrophulariaceae, Solanaceae, Boraginaceae, Asclepiadaceae, Apocynaceae, Myrtaceae, Melastomaceae, Cactaceae, Sapindaceae, Anacardiaceae, Euphorbiaceae, Rutaceae, Saxifragaceae, Papaveraceae, Nymphaeaceae, Chenopodiaceae, Polygonaceae, Proteaceae, Moraceae, Fagaceae, Salicaceae, Casuarinaceae; Zingiberaceae, Iridaceae, Amaryllidaceae, Bromeliaceae, Araceae, Palmae, Cyperaceae, Potamogetonaceae; Gnetaceae, Cycadaceae; Isoetaceae, Lycopodiaceae, Equisetaceae, Salviniaceae, Ophioglossaceae, Cyatheaceae, Hymenophyllaceae. The further orders studied will depend upon the object the student has in view, whether a general knowledge of botany, or a special knowledge of a particular flora, or of economic botany, &c. The treatment given to the orders in Part II. and the number of their genera and species will give a fair index to their importance.

There will be found in almost every botanic garden a *Range of Houses*, representing tropical and warm temperate climates, an *Arboretum* containing British trees and shrubs and others from similar climates, a *Herbaceous Ground* on which are grown herbs and small shrubs capable of outdoor cultivation in our climate, a *Pond* or *Tanks* for water plants, often fed by a running stream in which or on whose banks other plants may be grown, a *Rock-garden* for alpine plants, succulents, and others that love dry situations or stony soil, a *Bog-garden* for marsh and bog plants, and so on. There are special beds set apart in many gardens for *Agricultural* and *Medicinal* plants &c.

Whilst in the outdoor beds the plants are always arranged in the same way, this is not the case indoors. In summer most of the specimens from the cooler houses are carried out of doors and others from hot houses moved into cool. Again, in the houses themselves, with the exception to some extent of those at Kew, there is little attempt at any classification (whether morphological or according to country of origin) of the plants; they are put in the house best suited to their growth. Certain general principles only can be given to guide a student, and after a little practice, he will know fairly well where to look for a particular plant he desires to see. He will not, for instance, look for East Indian species on the Herbaceous Ground, or for Crassulaceae in the Bog-garden. He will know that few Australian plants, even from the south, are hardy in Britain and will seek them in the Temperate House, and so on.

The Range. Plant houses may be roughly classified into *general* and *special*, and these again into *tropical* and *temperate*. The general houses, such as the Stove or the Temperate House, contain plants of every kind to which the climate of the particular house is suited. The special houses, on the other hand, contain representatives of special groups (usually biological) of plants with certain features in common; such as the Succulent House, Tropical Orchid House, Waterlily House.

The following table gives a list of the various houses in the chief British gardens, showing the corresponding houses in each.

TROPICAL HOUSES

KEW*	CAMBRIDGE	OXFORD	EDINBURGH‡	GLASGOW	GLASNEVIN
Palm House Trop. Economics (11) Aroids (1) Begonias (8) Stove (9) Waterlily House (15) Victoria Regia (10) Trop. Ferns (2) (& in Aroids) Trop. Orchids (13) Succulents (5) (Stove, &c.)	Palm House & Stove Waterlily House Trop. Ferns Trop. Orchids Succulent & Cactus Houses (Trop. Orch.,&c.)	Palm House & Stove Waterlily House Trop. Ferns Orchids, Succulents (Stove, &c.)	Palm House Trop. Economics & Stove Aquatics Trop. Ferns Trop. Orchids, Succulents Nepenthes Ho.	Palm House Trop. Economics & Stove Waterlily House Trop. Ferns Trop. Orchids, Succulents (Waterlily Ho.)	Palm House & Stove Waterlily House Trop. Ferns Trop. Orchids, Succulents (Stove, &c.)

TEMPERATE HOUSES

KEW*	CAMBRIDGE	OXFORD	EDINBURGH‡	GLASGOW	GLASNEVIN
Temperate House Temp. Economics (12) S. African Plants (7) Conservatory (4) Temp. Ferns (3) Filmy Ferns (2a) Temp. Orchids (14) Alpine House (25) Insectivorous Pl. (14)	Temp. House & Conservatory Cool Ferns †Filmy Ferns †Cool Orchids (Succulents, &c.)	Old Succulent House & Conservatory	Temp. House Temp. Economics Conservatory Cool Ferns Filmy Ferns Cool Orchids, Alpine House Insectiv. Pl.	Winter Garden Heaths Rhododendrons Conservatory Cool Ferns, &c. †Filmy Ferns Interm. Orchids	Temp. House Australian Plants †Bulb House Conservatory †Filmy Ferns †Cool Orchids

* Numbers refer to Map of Kew Gardens sold at the Gates.   † Open only on application.

‡ The range, to include these houses, is at present (1896) in course of being rebuilt.

In the *Palm House* and *Stove* will be found tropical plants chiefly from climates where there is plenty of moisture, at least during a large part of the year. Here (and in the *Aroid House* at Kew) will be found most of the Cycads, Palms, Araceae, Bromeliaceae, Musaceae, Zingiberaceae, Marantaceae, Piperaceae, Moraceae, tropical Lauraceae, Leguminosae and Euphorbiaceae, Melastomaceae, Araliaceae, Sapotaceae, tropical Asclepiadaceae, Gesneraceae, Acanthaceae, tropical Rubiaceae and many smaller tropical orders. The contents of *Aroid, Begonia, Tropical Fern* and *Orchid Houses* are sufficiently indicated by their names. The *Water-lily House* contains various Nymphaeaceae, Hydrocharitaceae, and other tropical and sub-tropical water plants. In most gardens it is festooned with climbing plants, such as Vitis, Cucurbitaceae, Passifloraceae, &c. The *Cactus* and *Succulent Houses* contain xerophytes, chiefly succulent forms from very dry climates, including Cactaceae, Euphorbiaceae, Asclepiadaceae, &c. with fleshy stems, and various Liliaceae, Amaryllidaceae, Aizoaceae, Crassulaceae, Compositae, &c. with fleshy leaves (see Chapter III.). In these houses the air is kept much drier than in the preceding ones.

Turning now to the cooler houses, the *Temperate House* corresponds to the Palm House ; here will be found most Australian and other S. Temperate plants, the plants of the Mediterranean and warmer temperate zones, and the plants of the middle zones of the Himalaya and other tropical mountains. Most of the Proteaceae, Rutaceae, Thymelaeaceae, Myrtaceae, Acacias, &c. are here to be seen. The *Heath House* or *South African House* contains Ericaceae, Epacridaceae, &c., from the S. Temperate zone. The *Conservatory* is usually a show house, the plants in which are perpetually changed to keep up a display of flowers all the year round. The names of the other cool houses explain themselves.

The Arboretum contains specimens of trees &c., most of which belong to the orders Coniferae, Juglandaceae, Salicaceae, Betulaceae, Fagaceae, Ulmaceae, Magnoliaceae, Saxifragaceae, Hamamelidaceae, Platanaceae, Rosaceae, Leguminosae, Buxaceae, Aceraceae, Hippocastanaceae, Sapindaceae, Rhamnaceae, Vitaceae, Tiliaceae, Cornaceae, Ericaceae, Oleaceae, Caprifoliaceae.

The Pond, Tanks, and **Bog-garden** contain the hardy water and bog plants, especially those of the European flora. See Chapter III.

The Rock Garden contains most of the hardy alpine and rock plants, excepting those in the *Alpine House* (many alpines refuse to grow out-of-doors at low levels, on account of the dampness of the winter, and must be cultivated under glass for a portion of the year).

The Herbaceous Ground, lastly, contains all those smaller plants suited to ordinary out-of-door culture in this country, other than those requiring specially dry or wet situations. Here will be found representatives of most British plants, and foreign plants belonging to the same orders, and also many Commelinaceae, Nyctaginaceae, Phytolaccaceae, Aizoaceae, Capparidaceae, Zygophyllaceae, Rutaceae, Loasaceae, Asclepiadaceae, Polemoniaceae, Hydrophyllaceae, Acanthaceae, &c. Each order has usually a bed to itself, and the beds are grouped according to some system of classification (that of Bentham and Hooker in several gardens).

Visitors are not allowed to pick or handle specimens in botanic gardens, but in most of them specimens may be obtained for purposes of study by application to the Curator or sometimes to the Professor of Botany. At Kew there is a small Students' Garden, where specimens may be picked.

We shall now give a brief outline of a visit to the gardens of Kew and Cambridge, calling attention to the chief plants, families or groups of special interest. Details must be sought elsewhere in the book.

KEW GARDENS.

EVERY visitor should purchase the map (price *2d.*) sold at the Gates. There may also be had Guides to the three Museums (*4d.*, *4d.*, *3d.*), and the North Gallery of Paintings (*4d.*), and Hand-lists of various collections.

Entering from Kew Green, visit
Aroid House (No. 1).

> On N. wall &c. are climbing epiphytic Araceae, Vanilla, Piper &c. ; in centre Calamus, Chamaedorea, Anthurium &c.

Museum III. See special guide.

Trop. Fern House (2).

> Davallia epiphytic on right of entrance; down S. side are Lygodium, Tree ferns, Marattia, Adiantum &c.; returning on N. side, note Platycerium, Selaginella, Lycopodium &c.

Filmy Fern House (2a).

> Hymenophyllaceae &c.

Temp. Fern House (3).

> Marsilia on W. side, Gleichenia, Pellaea, Asplenium &c.

Conservatory (4).

> Ornamental flowering plants.

Succulents (5).

> Enter at S. end and go round. Going down E. side, note Sempervivums, Cotyledons, Crassulas *r.*; Agaves, Dasylirions &c. *l.*; quarter-way down Fockea *r.* Xanthorrhea *l.* then fleshy Senecios *r.*; half-way Testudinaria *l.*, Cacti begin *r.* mixed with Euphorbias &c., also *l.* On W. side Dyckia &c. *r.*, Euphorbia splendens &c. *l.* Then Aloe, Gasteria, Haworthia *r.* Leucadendron, Stapelia *l.* &c.

South African House (7).

> Go right round the whole range (7—14) and come out by same entrance. 7 contains Ericaceae, Mesembryanthemums, Pelargoniums and Cape bulbs (S. Temp.); 8 contains Begonias; in 9, note on *l.* Nepenthes, and various Palms, Cycads, Dracaenas, Melastomaceae &c.; in 10 are Victoria, Lodoicea &c.; 11 contains Trop. Economic plants, Trachylobium *l.*, Ficus indica, Anona, Castilloa, Cinnamomum, Toluifera, Tamarindus, Manihot &c.; in 12 are Temp. Economics. Returning through 11 note Anamirta on first pillar *l.*; pass through 10 into 13 and 14 (Orchids). At the far end of 14 is an annexe containing Insectivorous Plants (Sarracenia, Drosera, Dionaea &c). Return through 14, 13, 10, 9 (here note Bromeliaceae *r.* and Hydnophytum in hanging basket), 8, and out at end of 7 again.

Museum II. (Monocots. Cryptogams). See special guide.

Tank for Aquatics. See Water Plants (Chapter III.) &c.

Alpine House. See Alpine Plants (Chapter III.) &c.

Herbaceous Ground. Refer to Part II. for details of orders &c., and see Chapter III. A Hand-list is sold (price 1*s.*) at the Gates.

Rock Garden. See Alpine Plants, Xerophytes &c. (Chapter III.).

Museum I. (Dicots. Gymnosp.). See special guide.

Water-Lily House (15).

> Nelumbium, Nymphaea, Cyperus Papyrus &c. in tank; Hedychium in pots; climbing Cucurbitaceae on roof.

Palm House. We give a diagrammatic representation of the different beds in this house; the numbers signify the beds, the letters the window benches.

<pre>
                        Door
            Bench F   Bench B
        Bench G   13   5   Bench C
                     12   4
  S. Door   15   14 11   3   6   7   8   N. Door.
        Bench H   10   2   Bench D
                      9   1
             Bench E   Bench A
                        Main
                        Door.
</pre>
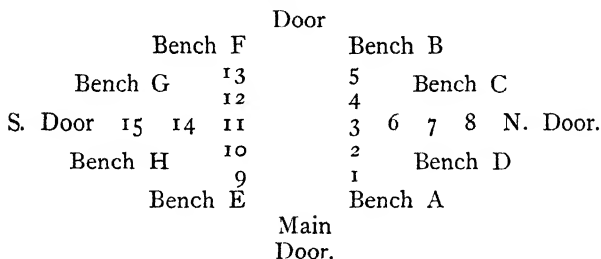
> In Bed 1 note Euphorbia at S. end, Myristica, Phytelephas, Cycads, Musas. In 2, Caryota, Howea, Calamus, Acanthorhiza, Thrinax, &c. In 3, Sabal, Cocos, Bambusa. In 4, Arenga, Livistona. In 5, Eugenia, Carludovica, Smilax, Phoenix, Ficus, Cyclanthus &c. In 6, Cycads, Cocos nucifera, Pandanus. In 7, Pandanus on W. side. In 8, Scheelia &c. Benches A, B contain Cycads and small Palms, C contains Trop. As., D Trop. Amer. plants (Bauhinia up S. angle of roof).
>
> In the S. half, in bed 9 note Theobroma, Freycinetia, Musa, Piper &c. and several epiphytes with Renanthera on a tree in S.E. corner. In 10, Elaeis, Lodoicea. In 11, Ravenala, Rhapis, Bambusa. In 12, Chrysophyllum, Sabal. In 13, Durio, Wallichia, and Vitis polystachya (flat-stemmed liane). In 14, Theophrasta, Brownea, Heritiera, Couroupita and Cycads. In 15, Cycads &c. The benches E, H bear American plants, F small Eastern Palms, and G, African plants.

Temperate House. The beds are numbered thus:

<pre>
            Bench D   Bench B
                     16   6
            17   15   5   7
   South   18   14   4   8   North
   Octagon   19   13   3   9   Octagon
                     12   2
            20   11   1   10
            Bench C   Bench A
                        Main
                        Door   (facing Pagoda Vista)
</pre>
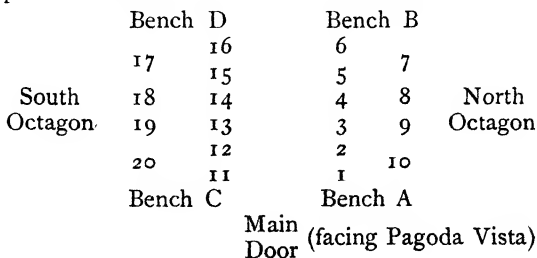
In Bed 1 note Asparagus, Nerium, Yucca, Acacia, Myrtus, Dicksonia, Cocculus, Davallia, Phormium. In 2, Agathis, Myrsine, Thea, Callitris. In 3, Camellia, Araucaria, Diospyros, Dracaena, Cyathea, Olea. In 4, Pinus, Musa, Bucklandia, Alsophila. In 5, Jubaea, Camphora, Podocarpus. In 6, Smilax, Eucalyptus. In 7, Alsophila, Todea and other ferns. In 8 and 9, Camellia. In 10, Rhododendrons of the Himalaya. In N. octagon, Celastrus, Zanthoxylon, Combretum, Prionium, Gardenia, Citrus &c. round sides, and Grevillea, Hakea, Yucca, Banksia, Euphorbia, Ficus religiosa, Acokanthera, Gnidia, Olea europaea, Vitex, Aloe &c. in centre. Bench A bears plants from the Andes, Mexico, Canaries and S. Africa; B bears N. Indian and E. As. plants.

In S. half, in bed 11 note Myrsiphyllum, Ficus elastica. In 12, Alsophila. In 13, Phoenix. In 14, Phytolacca, Olea, Pittosporum. In 15, Eucalyptus Globulus, Cephalotaxus, Morus, Tmesipteris (on a tree fern). In 16, Callistemon, Bomarea, Magnolia, Strelitzia. In 17, Protea, Illicium, Acacia, Eucalyptus. In 18, Pitcairnia, Fuchsia. In 19, Carica, Smilax. In 20, Juniperus, Lardizabala. On bench C, Australian plants, on D, New Zealand plants; note phyllodineous Acacias &c.

North Gallery (paintings of vegetation in different lands). See special guide, and Chapter III.

Arboretum: to the contents of this the map should be a sufficient guide. [Hand-list of Polypetalae, 8*d.*]

BOTANIC GARDEN, CAMBRIDGE.

Enter from Trumpington Road and turn to left.

On *r.* is the *Pond* (water and marsh plants), *l.* Aesculus, Acer &c. Then Rubus *r.* Calycanthaceae *l.* In the *Dell* note Cyperus Papyrus, &c. Going towards the range, Celastraceae, Rhus &c. *r.* Magnolia *l.* *Bog-garden r.* (admission only on application). Salix and Populus *r.* Turn along centre walk to *r.* On *l.* are tree Rosaceae, on *r.* Rosa &c. At corner of main walk, Cedrus Libani *l.*, Cupressus &c. *r.* Enter *Herbaceous Ground.* Turn *l.* at far side. Then on *l.* are tree Leguminosae (Gleditschia, Cercis, Colutea &c.), then Vitaceae and Caprifoliaceae *l.* Go round the *Pinetum* and *Rockery* and enter *Range* at E. end. In *Cactus House* note Cacti, Euphorbias, Stapelias &c. In *Succulent House* are Aloe, Gasteria, Haworthia, Crassulaceae, Mesembryanthemum &c., and insectivorous plants. In *Trop. Orchid House* note orchids, and Nepenthes, Utricularia (in baskets) &c., and a collection of epiphytes on tree facing door. In *Trop. Fern House*, Platycerium &c. as at Kew. In *Palm House*, Phoenix facing door; turn *r.* Aroids, Bromeliaceae &c. *r.*, Palms, Pandanus &c. *l.* Musa *l.* as enter *Waterlily House.* In this note Cyperus Papyrus, Nelumbium, Nymphaeas, climbing Cucurbitaceae, Mimosa, Vitis gongylodes &c. Returning to Palm House note Dioon, Cycas,

&c. *l.*, Ficus religiosa *r.*, Acacia sphaerocephala *l.* Musa *l.*,
Monstera *r.* In *Stove*, Saccharum facing door. Coffea *r.* Ananas
r. with Cola, Strychnos, Piper &c. then *r.* Castilloa, Haematoxylon,
Caryophyllus, Dichopsis, Maranta &c. In centre *l.* Galactodendron,
Xanthosoma. At end *r.* Goethea. In *Conservatory*, show plants.
In *Cool Fern House*, Asplenium Nidus *r.* In *Temp. House* Todea
facing door, Cobaea on first pillar. Looking into centre from far
end see many Austr. plants, e.g. Casuarina, Eucalyptus Globulus *r.*
Grevillea *l.* By end door Rubus australis, Acacias &c. The other
houses are only open on special application.

The above are not in any way intended as *guides* to
these gardens, but as sketches of routes through them,
calling attention on the way to a few of the more note-
worthy plants &c. Space will not permit of any description
of the remaining British gardens, but they resemble the two
described in most features.

BOTANICAL MUSEUMS.

These are arranged in various ways, to illustrate 'scientific'
or 'economic' Botany. In the latter case, and often in the
former, the specimens are usually grouped under the natural
orders to which they belong. Other museums exhibit series
of specimens illustrating particular types of vegetation, special
morphology of stems &c. In either case, this book will be
found available, but for the details of economic products,
other books should be consulted, e.g. Müller's *Select Extra-
tropical Plants*, *Treasury of Botany*, *Guides to the Museums
of Kew*, &c. See Chapter IV.

CHAPTER I.

OUTLINES OF GENERAL MORPHOLOGY AND NATURAL HISTORY OF PHANEROGAMS AND FERNS.

IN this chapter an attempt is made to give such an outline of these subjects as may help to guide anyone in studying them in a botanic garden or in the field, and such as may also serve in rendering more intelligible the later chapters, where a knowledge of the elements of these subjects is taken for granted. The outline can be filled up in detail by reference to Part II. and by the actual study of the plants.

Until lately, morphology has been a most formal science, and this formality still survives in the text-books most commonly in use. The older workers started from the flowering plants and even from the higher types of these, and either neglected the lower types of vegetation, such as ferns &c., or treated them in a summary way as 'exceptions' to which the 'laws' and 'rules' of morphology were not applicable! It is now recognised that this method of procedure is erroneous, and that the morphology of the higher plants can only be understood by reference to, and should be expressed in terms of, that of the lower. At the same time we must beware of starting too low in the scale, for there is a great gulf between the Pteridophyta and the Bryophyta, the leafy plant in a fern not being the equivalent of that in a moss or liverwort (see Pteridophyta in Pt. II.). The Pteridophyta (ferns &c.) and Spermaphyta (flowering plants proper) however, may fairly be treated together. Most text-books deal with morphology apart from physiology or any other branch of botanical study, thus rendering it

extremely dry and unintelligible. A particular 'type' of stem, for example, is chosen and described and then other varieties are treated of in order under the title of 'modified' or 'metamorphosed' stems, and so on. In the treatment of the subject here given, we shall endeavour to indicate a little more clearly the connection between morphology and other subjects, by dealing in a general way, first of all, with the various parts of a plant, and then (in Chap. III.) with a number of different types of vegetation, which illustrate very clearly how closely the morphology of a plant is bound up with its physiology, its geographical distribution, its relationships to other plants and so on. [The student who is interested in this subject would do well to read Asa Gray's *Structural Botany* as an example of the formal morphological work, and the introductory chapters of Sachs' *Lectures on Physiology* as illustrating the rebound to the opposite extreme of 'physiological morphology'; also Sachs' *History of Botany.*]

It is customary and convenient to classify the various parts or organs of plants under the two headings of *vegetative* and *reproductive* organs. The former are those devoted primarily to purposes of growth, concerned chiefly with the life of the individual, and include the root, stem, and leaf, the latter are those devoted primarily to reproductive purposes, concerned chiefly with the life of the race, and include the flower, fruit, and seed. A hard and fast line cannot be drawn. Vegetative reproduction (see below) is a common phenomenon in plants, and often the reproductive organs aid in nutrition. In the lower forms (*e.g.* many ferns) the same organs serve both purposes.

The leafy plant as we see it in Phanerogams or in Ferns is a highly differentiated body, with vegetative and reproductive parts and with root, stem, and leaf. To obtain a clear idea of the morphology and of the real meaning of these structures, it may be well to trace in brief outline the probable evolutionary history of the plant, from its simple beginnings through the more and more complex forms which it gradually assumed. Of course, as in all statements as to evolutionary progress, we can only speculate, with more or less degree of probability, upon the course of events.

In the seaweeds (Algae), the modern representatives of the oldest and lowest division of plants, the plant lives in water, and usually goes through a simple life-history which may be represented by the following diagram :

Plant → $\left\{ \begin{array}{l} \text{antheridium} \rightarrow \text{spermatozoid} \\ \text{oogonium} \rightarrow \text{ovum} \end{array} \right\}$ zygote → Plant.
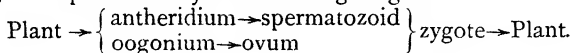
The plant bears sexual organs, which give rise to male and female cells (*spermatozoids* and *ova* respectively); these are often termed *gametes*, and the plant bearing them the *gametophyte*. The two gametes when fused together give a cell, the *zygote*, which after a longer or shorter period grows into a new gametophyte. Here every successive generation is sexual; there is no alternation of an asexual between each two sexual generations. In Coleochaete and a few other forms, however, the zygote breaks up into a number of cells, and each of these may germinate and give rise to a new gametophyte. Here then we find, perhaps, an indication of the first appearance of the *sporophyte* or *asexual gene-ration* in the life-history—a few neutral cells interposed between two successive gametophytes. The next stage in the upward progress is probably nearly represented at the present day by some of the simpler liverworts, *e.g.* Riccia. Here the ordinary plant is sexual, but the zygote developes into a *spore-capsule* or *sporogonium* (seen in its highest form in the larger mosses). This is attached to the gametophyte by an organ termed the *foot*, through which it receives its nourishment, and its whole contents go to form *spores* or *asexual* reproductive cells. Each of these on germination gives rise to a new plant (gametophyte). In this life-history there is a clearly marked *Alternation of Generations*, as may be diagrammatically shown thus :

Plant → $\left\{ \begin{array}{l} \text{antheridium} \rightarrow \text{spermatozoid} \\ \text{archegonium} \rightarrow \text{ovum} \end{array} \right\}$ zygote → sporo-gonium → spore → Plant.
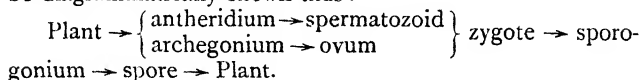
Zygote and sporogonium represent the sporophyte, the rest the gametophyte. It is to be noted that in its earliest stages *the sporophyte is reproductive only*. This was indicated in Coleochaete ; in Riccia there is a slight amount of vege-tative tissue (foot &c.), but there must have been many intermediate steps. The liverworts and all the higher plants are distinctly land plants, so that the further evolution must

have taken place on land. From the stage just considered, upwards to the highest flowering plants, there is a steady increase in comparative size and importance of the sporophyte, at the expense of the gametophyte. In the higher liverworts we see some of the tissue, which in the lower goes to form spores, rendered sterile and vegetative; the plant is thus able to assimilate a good deal of its own food. In these sporophytes we find a distinct division of the various functions amongst distinct portions of the plant. In other words *physiological division of labour* appears. The earliest sporophyte was uniform in structure and its function was chiefly reproductive, its life being very brief; in Riccia there is an advance in size, but no differentiation is yet clearly visible, and the sporophyte is parasitic. As we proceed upwards, the sporophyte is seen to become less dependent upon the gametophyte, and thus it has two functions to perform— nutrition and reproduction. Part of the food even in the highest liverworts comes from the sexual plant and is absorbed by an organ termed the foot; the rest is taken from the air and dealt with by the green sterile tissue of the capsule. We thus see a clear indication of a differentiation of the originally simple uniform organism into three parts with different functions—reproduction, absorption, assimilation. The next stages are difficult to follow in detail, as the gap between Bryophyta and the lowest Pteridophyta is very great. We may, however, probably accept the view that the next step was that the sporophyte became independent of the gametophyte and lived its own life upon the soil and that now the root became more clearly differentiated from the shoot, whilst the latter began to show a more or less clear distinction into reproductive and vegetative (assimilative) parts. At first uniform in its structure, the shoot also began to show a distinction into *stem* and *leaf*, the performance of the important functions of assimilation and reproduction being carried on by the latter, whilst the former served as a highway for food materials between root and leaf and as a means of spreading out the leaves to advantage. It is obvious that, other things being favourable, a certain amount of actual tissue when formed into a stem and leaves will have a great advantage over a similar amount in a solid mass, on account of the much increased area spread out to

light and air.   Even in the lowest Pteridophyta, *e.g.* Phyllo-
glossum, the sporophyte is clearly distinguished into root,
stem, and leaf, and in the higher forms the stem is also
more or less branched, which of course further aids in the
spreading out of the leaves and enables a greater number to
be borne on one plant.   [For details of the life-history and
Alternation of Generations in these higher forms, see articles
Pteridophyta and Phanerogamae in Part II. where further
references are given.]

Let us now follow the further differentiation of the re-
productive function from the vegetative.   In the tissues of
the simple spore-capsule of a higher liverwort, the cells per-
forming these two great functions are not widely separated.
In the Pteridophyta the reproductive function is confined
to the shoot, and, with rare exceptions, to the leaves.   In the
lower groups, *e.g.* Filicineae Eusporangiatae (q.v.), the same
leaf performs both reproductive and vegetative functions,
though the leaf may (as in Ophioglossum) be differentiated
into two parts, each with its own function.   [This pheno-
menon may be traced all through the Filicineae Leptospo-
rangiatae, or true Ferns; in most of them the sporangia are
on the ordinary leaves, but more or less differentiation occurs
in Osmunda, Aneimia, Lomaria &c. &c.   The Ferns are
probably not in the direct upward line of evolution, but are
an offshoot; see Chapter II.]   Higher in the series *e.g.* in the
Lycopodinae, the separation becomes clear—into leaves,
which are purely vegetative (*foliage-leaves*), and leaves which
bear sporangia (*sporophylls*).   The latter, too, are confined
to one portion of the stem, and occupy it to the exclusion of
any vegetative leaves.   We have here the first indication of
a differentiation of the whole shoot into a vegetative part
and a reproductive part.   The latter we may term the
inflorescence.   In the higher Pteridophytes, this is repre-
sented by the little *cone* or *strobilus* at the tips of most of
the shoots.   In the Gymnosperms it is very similar, but
rather more obvious.   In many Angiosperms also, the
inflorescences are scattered over the vegetative shoots as
terminal portions or as lateral branches, but in other
cases they are aggregated together into large masses
terminating the main vegetative shoot, as in some Palms &c.,
and in many herbaceous plants.   In many plants with rhi-

zomes below ground, the inflorescence arises as a shoot from the rhizome, quite independently of the vegetative shoots, and is thus very strikingly differentiated in appearance. This is seen in species of Equisetum, many Zingiberaceae (*e.g.* Mantisia), *Anona rhizantha*, and other plants.

The upward progress of the sporophyte is accompanied by a reduction of the gametophyte. In the Algae the latter is the *plant* and so also in Liverworts and Mosses. In the Ferns it is much smaller than the sporophyte but still capable of independent growth; in the Lycopods it is smaller still, and in Phanerogams it is no longer free of the sporophyte, but enclosed in and parasitic upon it, and reduced to a few cells (see articles Pteridophyta, Phanerogamae &c.).

When the reproductive portion of the shoot has become clearly differentiated off from the vegetative, the latter is much more amenable to variations in form and structure which, when the separation was incomplete, might have interfered seriously with reproduction. To this is probably to be ascribed the enormously greater variety in the morphology of the shoot in Phanerogams than in Pteridophytes. The one comparatively modern genus Senecio shows as much variety in form as all the latter put together. It is very important to clearly recognize this fact of the great variability of the vegetative shoot ; we shall deal with this subject again in the next chapter.

To sum up briefly, the sporophyte was at first *undifferentiated, and reproductive only*. Then it showed differentiation into an absorptive *root* and reproductive *shoot*, and the latter began to differentiate its vegetative and reproductive functions; it also became divided into *stem* and *leaf.* The latter at first performed both functions, but gradually the vegetative leaves (*foliage*) became distinct from the reproductive (*sporophylls*) and the latter, being aggregated together upon the stem, formed a distinct part of the shoot (the *inflorescence*) whose primary function was reproductive, distinct from the vegetative part of the shoot. The latter now became very much more liable to variation in structure to suit the different requirements of life in different climates, and situations, or for other purposes.

What we have said above is of course to some extent

speculative, but it was very probably the course of events, and will at least serve to emphasise the meaning of the shoot and its parts as we find them in the higher plants, by indicating the chief functions they perform, and the *morphological differentiation of parts which accompanies the physiological differentiation of functions*. The four chief functions performed in a highly organised plant, *viz.* absorption of food from the soil, assimilation, transport of materials, and reproduction, are chiefly performed by root, leaf, stem and inflorescence respectively.

VEGETATIVE ORGANS.

The sharp distinctions formerly drawn between root, stem, and leaf cannot now be maintained as constant, in view of recent discoveries (see Neottia, Anthurium, Utricularia), but the terms remain convenient for use in grouping the parts of plants. The two last are better considered together under the common term *shoot*, the distinction between which and the *root* is usually clearly marked even in the embryo (plumule and radicle in seeds, or diametrically opposite cells in the embryo of a fern). The root usually grows downwards into the substratum for the purposes of absorbing food substances and of anchoring the plant; this however is only its physiological description—morphologically speaking it is that member of the plant body which does not bear lateral members (branches) differing from itself (*i.e.* does not bear leaves nor the true reproductive organs), is endogenously developed (at least in its branches) and usually bears a root-cap (see below). The shoot on the other hand (or at least part of it) usually grows above ground and consists in part of green tissue performing assimilatory functions; it is that member which does bear lateral members differing from itself (often leaves, and always the true reproductive organs), is exogenously developed (at least in its branches) and has no cap, but very often a bud of young leaves. It may also bear roots, endogenously developed from its tissues.

The Root. Living, as it usually does, below ground and, therefore, under conditions which do not offer much variety, the root exhibits a great uniformity of structural

and functional characters throughout the various families of the flowering plants and ferns. There is however a certain amount of variety even among subterranean roots, and still more in those roots which are formed above ground (*aerial roots*). The latter are usually formed upon stems or leaves; such roots, together with branch roots formed upon other roots but not in acropetal succession (see below), are classed under the term of *adventitious roots*, whilst the original root derived from the embryo together with its normal branches (those formed in acropetal succession) are spoken of as *true roots*. Morphologically speaking, there is little objection to these terms, but it must be recognised that there is no essential difference in structure or function, but only in mode of origin, between them.

If the development of the root in a pea or bean seedling be studied, a good general knowledge of the various structural and functional phenomena of roots may be obtained. The root emerging from the seed at once bends downwards, enters the soil and forces its way downwards as nearly as possible in a vertical direction. This is due to the influence of gravity upon the growing tip of the root, which endeavours always to grow towards the centre of the earth; if it be forcibly deflected from this course, *e.g.* by a stone, it returns to it as soon as possible. We express this property of the root by saying that it is *positively geotropic*, but this and similar terms are very liable to be misused as concealments of our ignorance of anything beyond the mere fact that the root does behave in a definite way under the influence of gravity. Gravity however, though the chief, is not the only stimulus influencing the growth of the root; if the soil on one side of the root be damper than on the other, the root will.be deflected towards the damp side, or in other words will exhibit positive *hydrotropism*. The root is also sensitive to light, and bends away from it in most cases, *i.e.* is *negatively heliotropic*.

The downward growth of the root is effected by the formation of new cells at the growing point; this is not at the extreme tip, but a very small distance behind it, being covered by a mass of cells that is continually renewed from within, as it wears away outside, by the growing point itself (cf. the renewal of the skin of the hand); this pro-

tective sheath is called the *root-cap* and is very nearly always present on roots (see Azolla and Neottia), even in aerial or water roots where it can be of little or no use, though it is of scientific importance as showing that these roots are probably derived from land roots.

From the main root of a bean there sprout lateral roots arranged in four vertical ranks (*i.e.* if some of them face N., the others will face some E., some S., some W.). This arrangement is due to the fact that they arise from the tissue of the pericycle, deep down in the main root, at points opposite to the xylem bundles, of which there are four. The young root burrows its way out through the cortex of the parent root into the soil; such development is termed *endogenous*, in contrast to the *exogenous* development, from superficial cells, of the branches of the shoot. The lateral roots are also arranged in a definite order of age, the youngest being nearest to the apex of the main root; this is termed arrangement in *acropetal succession*, and a branch-root arising at a later period, not in this succession, is termed adventitious. The lateral roots grow out from the main root in definite directions; they are but little sensitive to gravity and grow more or less horizontally, but they are governed in their growth by definite though ill-understood laws. If, for instance, the northward growth of one of them be interrupted by a stone, the root, as soon as it has reached the edge of the obstacle, once more resumes that direction of growth. This phenomenon, the tendency of lateral roots to grow away from the main root, is termed *exotropism* and is obviously of much importance to the root by enabling it to make the best use of the soil in which it is growing. The lateral roots may be again branched and these *roots of the third order* are exotropic with regard to those of the second, and so on, so that here we have cases of roots actually growing in a direction quite contrary to that impressed by gravity upon the main root. These branches may in some cases appear above the soil, *e.g.* in mangroves (see Ch. III.), Taxodium, &c.; in these cases they have assumed an aerating function and do not perform the usual root functions to any extent (see also Jussieua, Sesbania, Rumex). The reason that roots are not often seen above the soil is the dryness of the air (so that hydrotropism is active), but if

the air be kept saturated, roots can easily be made to appear above the earth.

The functions most characteristic of roots are the absorption of food-materials from the substratum, and the anchorage of the plant therein. The former is generally effected by the agency of the fine unicellular *root-hairs* which clothe the tips of the roots a little way behind the actual apex. By these the water held by capillary attraction around the particles of soil is taken up, and in it are contained various mineral substances (sulphates, nitrates, chlorides, phosphates, carbonates &c.) from which the plant gets the elements it requires for its food, with the exception in green plants of the carbon, taken in by the leaves. The branching and mode of growth of the root above described admirably fit it for the absorption of all the food-materials obtainable in the soil in which it grows. In a few cases other phenomena of absorption are seen. In saprophytic plants (see Ch. III.) the root absorbs the products of decaying organic matter (*humus*) from the soil, as well as mineral salts. In most of our forest trees and in many other plants, the root hairs are replaced by a fungus whose hyphae absorb in the same way. This is termed a *mycorhiza*; in the Fagaceae, Betulaceae, Coniferae, &c. it is *ectotropic, i.e.* the hyphae do not enter the cells of the root but run between the epidermal cells, whilst in Orchidaceae, Ericaceae &c. it is *endotropic*, the hyphae entering the cells. [See Ludwig's *Biologie* for details.] Mention may also be made here of the tubercles of the roots of Leguminosae (q.v.) and other plants. In a few cases the roots are *parasitic* upon other roots living in the same soil, and are modified in structure to suit this modification of their absorptive functions. The second great function of the root, anchorage of the plant, is admirably effected by the branching and arrangement of the roots, aided by their internal mechanical adaptation, the vascular tissue being centrally placed so as best to resist a longitudinal strain. The growth in thickness of the root keeps pace with that of the stem. In many large trees the growth in thickness of the lateral roots at the base of the trunk is chiefly vertical, and 'buttress' roots, so well seen in Ficus, are thus formed.

So far we have been dealing primarily with the case of

a long main root (*tap-root*) with lateral branches. This is common in Dicotyledons and Conifers, but a second type is frequent and is the rule in Monocotyledons, viz. the *fibrous* root, well seen in grasses. Here the main root soon ceases growth and from the base of the stem others are formed (adventitious) which spread out into the soil, all growing to about an equal length and thus forming a tuft of roots. Plants with this type of root are usually herbaceous, but a few are of large size and in these cases the need for additional anchorage is met by the formation of 'flying-buttress' roots which spring from the stem at some height above the soil and grow more or less obliquely downwards (see Pandanus, Palmae, Ficus &c.). The 'pillar' roots of *Ficus indica* also belong to this class. These last mentioned roots are obviously at first aerial roots, and lead on naturally to a consideration of other cases, such as the aerial nutritive roots of many Araceae (q.v.), which finally reach the soil, those of Orchidaceae, which do not, the clasping and climbing roots of Araceae, Hedera, Ficus &c. (q.v.), the thorn roots of Acanthorhiza, Iriartea, Myrmecodia, the parasitic roots of Cuscuta, Viscum &c. and so on. These are dealt with under the orders or genera to which they belong and also in Chapter III.

A function often performed by roots, and one which seriously modifies their structure, is that of storage of reserve-materials to enable the plant to start growth in the wet season, or in the next spring &c. (see *Herbs* and *Trees* in Ch. III.). The root is usually thickened to contain the materials, and may assume a form very different from that of a non-storing root. (See Brassica, Raphanus, Daucus, Orchis, Dahlia, Taraxacum &c.).

Roots in a few cases contain chlorophyll and are thus able to act as assimilating organs. This function assumes considerable importance in many epiphytic Orchidaceae, and in that curious family of water-plants the Podostemaceae, whose vegetative organs consist entirely of roots.

Lastly, mention may be made here of the fact that a number of plants are entirely without roots, the usual root-functions being performed by portions of the shoot; such are Psilotum, Salvinia, Aldrovanda, Utricularia.

Exceptional features of interest in roots are dealt with in

the articles upon Velloziaceae, Taraxacum, Isoetes &c. in addition to those mentioned above.

The Leaf. Most text-books deal with the stem before the leaf, but there is much to be said in favour of a reversal of the order; the leaf is the more important of the two, performing the more important functions. These are, (1) the great function of *assimilation*, (2) *transpiration* and (3) *storage* of reserve-materials; other functions are sometimes performed by leaves in exceptional cases, *e.g.* the capture of flies in Drosera &c., or the absorption of food from the substratum in Salvinia, and of course, like other living cells, those of the leaf respire. Leaving for the present the consideration of the external form of the leaf, let us deal briefly with its internal construction as illustrated by any of the commoner field-plants of Britain; for, as we shall see, plants of different climates &c. exhibit very great differences in the form and structure of their leaves. This will aid us in the subsequent consideration of the functions of the leaf.

Upon the upper and lower surfaces of the leaf is a layer of cells, usually one deep, known as the *epidermis.* Below the upper epidermis is the *palisade-tissue,* formed of large cells containing chlorophyll (the green colouring matter of plants), arranged with their long axes at right angles to the epidermis. Below this layer is the *spongy tissue,* also formed of green cells, very irregularly arranged in a network, with large and numerous intercellular spaces containing air. This air communicates with the atmosphere by means of openings in the epidermis, known as *stomata,* chiefly or only found upon the lower side of the leaf. Every cell of the leaf is thus placed in direct contact with the air (for details of structure see any elementary text-book). Now it is found that, in presence of light of sufficient intensity, with a suitable temperature, the chlorophyll-containing cells of plants are able to make use of the carbon dioxide gas of the air, using the carbon in the construction of the complex materials of the plant and returning oxygen to the air. This process is termed *assimilation,* and is perpetually going on in all green parts of plants when the conditions are favourable. With the chemistry of the process we are not here concerned. The cells of the leaf being in direct contact with the air and also very thin-walled, it is evident that consider-

able evaporation of the water contained in them must take place. This process is called *transpiration*, and is of great importance, as it determines the upward flow, from the roots to the leaves, of the water absorbed by the former, containing in solution the various food-materials of the plant, which are needed in the leaves to carry on the process of assimilation. This water travels in the *wood* or *xylem* of the vascular bundles of the root and stem. In the leaf the one or few bundles that enter it from the stem commonly branch out a great deal, forming what are known as the *veins* or *nerves*. These, as may easily be seen in a skeletonised leaf picked up in winter, branch and rejoin repeatedly, thus forming a fine network all over the leaf. In the meshes of the network may be seen the final endings of the bundles as little blind branches. These run among the green cells and consist even at their smallest of a *xylem* and a *phloem* portion; the former supplies water to the assimilating cells, the latter carries away the products of assimilation to other parts of the plant. Except in the finer ramifications the vascular bundles in the leaf are usually accompanied by a certain number of *fibres* whose function is primarily mechanical, the bundles being rendered elastic and comparatively rigid by their presence, so that the thin and delicate green parts of the leaf are stretched out smoothly and are also less liable to injury by tearing.

A consideration of the above statements will show how admirably the structure of a leaf is suited to the performance of the two great functions of assimilation and transpiration, the very maximum of cell-surface being exposed to the air with the minimum of waste or of mutual interference of parts. Such, or something like it, is the structure of most leaves growing in sunny places with a plentiful supply of water from the roots. In very dry climates the transpiration would be too great for the water supply and the structure has to be modified to suit the new conditions (see Xerophytes, in Chapter III.). Similar considerations explain the other modifications of structure found in water-plants, &c.

The function of storage of reserve-materials is only performed to a very slight extent by such a leaf as we have described; the rapidity of assimilation during the day causes a temporary excess of the products, which are stored in the

cells till night comes on, when they are carried away. Such a small demand on the capacity of the leaf causes no appreciable effect upon its general structure, but in many plants the systematic storage, for long periods, of large quantities of stuff, is undertaken by the leaves, which then usually exhibit a more or less fleshy or succulent character. See Chapter III. (Herbs, Xerophytes, &c.).

Respiration is carried on by all the living cells of the leaf, as by other living cells; it consists in the absorption of oxygen from the air and the consequent decomposition of some of the protoplasm of the cells with the evolution of carbon dioxide. The access of air to the leaf-cells for purposes of assimilation favours respiration also, and as far therefore as the influence of function upon structure is concerned we may leave respiration out of account.

The other functions performed by leaves are comparatively of little importance in a general review, for they are only found in small groups of plants, such as climbers, water-plants, &c. (see Chapter III.).

The external form of leaves presents extraordinary varieties in different groups of plants, even in nearly related forms, and we are at present almost entirely ignorant of the factors determining the shapes, &c. The leaf commonly shows a distinction into the *leaf-base* or portion abutting on the stem, the *leaf-stalk* or *petiole*, and the *blade* or *lamina;* attached to the base are often found a pair of *stipules*, one on either side.

[*Technical terms used in the description of leaves.* A few of the principal of these are here given; for details see Lindley's *Descriptive Botany* or Asa Gray's *Structural Botany*. With regard to its *insertion* or mode of union with the stem the leaf may be *petiolate* or *sessile* (*i.e.* with or without stalk respectively), *amplexicaul* (clasping the stem at the base), *sheathing* (as in Grasses, the leaf-base forming a tube round the stem), *perfoliate* (the leaf united round the stem, as in Bupleurum), *decurrent* (continued by a wing on the stem, as in thistles), &c. It may be *stipulate* or *exstipulate* (with or without stipules respectively); the shape &c. of the stipules is described as if they were leaves. The *venation* (arrangement of the veins) may be *pinnate* or *palmate ;* in the former case there is a *midrib* with lateral veins branching from it, in the latter several equal veins spread out in the leaf like the fingers of a hand but all from one point. The further ramification of the veins is described by the terms *net-veined* (irregular meshwork, as in most Dicotyledons), *parallel-veined* (meshes more or less rectangular, as in most Monocotyledons), *fork-veined* (veins forking into two, as in

Ferns). Leaves are divided into *simple* and *compound*, according as the stalk bears one or several separate *leaflets*. In the latter case the leaflet is described as if it were a leaf. The leaf (or leaflet) may be *entire* (without notches in the margin) or may be more or less incised. If the margin has small teeth pointing forwards, it is *serrate*, if pointing outwards, *dentate;* if the teeth are rounded but the notches sharp, the margin is *crenate*, if both teeth and notches are rounded, it is *sinuate*. If the depth of the divisions is equal to ¼ the distance from midrib to margin, *i.e.* if the incisions are conspicuous in proportion to the size of the blade, other terms come into use. If the notching is from ¼ to ½ the depth, the leaf is *-fid*, if ½ to ¾, *-partite*, if over ¾, *-sect*. Prefixes of *pinnati-* or *palmati-* are always used before these terms to express the particular form of notching, which depends upon the venation. The portions into which the leaf is thus divided are termed *lobes* or *segments*. If the division reaches completely to the midrib, the leaf is compound, and is then said to be *palmate* or *pinnate* as the case may be. If there are just 3 leaflets the leaf is usually called *ternate* (*e.g.* clover); pinnate leaves may be *equally* (*pari-*) *pinnate* (with an even number of leaflets) or *unequally* (*impari-*) *pinnate* (with an odd leaflet at the end). The shape of the leaf-blade itself, if simple, or the outline of a compound leaf, may be *needle-shaped* or *acicular* as in Pinus, *linear* (very long and narrow as in Grasses), *lanceolate* (about 3 times as long as broad, tapering gradually towards the tip), *ovate* (about twice as long as broad, and tapering towards the tip), *cordate* (similar, but heart-shaped at the base), *elliptical* (tapering equally to base and tip, and somewhat narrow), *oval* (*do.* but wider), *oblong* (sides parallel for some distance, the ends tapering rapidly), *reniform* (kidney-shaped), *orbicular* (circular in outline; if the petiole is inserted at the middle of the blade, as in Tropaeolum, this leaf is termed *peltate*), *hastate* (with two pointed lobes sticking out horizontally at the base), *sagittate* (two lobes projecting towards the stem), *spatulate* (spoon-shaped, as in daisy), &c. If a leaf be of lanceolate shape but the gentle tapering be towards the base, it is called *oblanceolate*, and so also leaves may be *obovate*, &c. The apex of the leaf may be *acute* (pointed), *obtuse* (blunt), *acuminate* (tapering in hollow curves to a long fine point), *emarginate* (notched), *mucronate* (with a stiff point on a nearly straight edge, thus ‿‿), &c. The surface of the leaf, as of other parts, may be *glabrous* (without hairs), *downy* (with soft hairs), *hairy* (coarser hairs) or *hispid* (rough bristly hairs). Leaves may further be *evergreen* or *deciduous* (falling in winter); in the latter case they may be *articulate* (cut off by a special absciss layer and falling early in winter), or *non-articulate* (hanging on to the stem, though dead, for an indefinite period, as in beech hedges, oak &c.). The *vernation*, or folding of the leaves in the bud, is described as in flower-buds (q.v.).

When a character is not accurately described by one of the terms given, but is rather half-way between two, both are used; thus a leaf may be linear-lanceolate or ovate-cordate. As an example of the use of these technical terms, we quote from Lindley the descriptions of two leaves:

Lilac: leaves opposite, exstipulate, roundish-cordate, very acute, thin, smooth, rather longer than the linear channelled petiole.

Garden Strawberry: leaves all radical, ternate, dark-green, somewhat shining, very coarsely serrated; with strong parallel oblique veins, silky beneath; leaflets nearly sessile, roundish oblong, entire towards the base, shorter than the semi-cylindrical hairy petioles; stipules membranous, lanceolate, acuminate, half adnate.

The terms opposite and radical are explained below.]

In the Ferns, the leaf being still concerned with reproduction is, as we have mentioned, but slightly variable, but among the higher plants the now purely vegetative leaf shows an extraordinary variety in form, and is frequently found performing novel functions, or those usually carried on by other parts of the plant.

Even on the same plant the form of the leaf is by no means always the same; some of the leaves may exhibit a different structure from the rest. In such cases of *polymorphism* as Capsella, Bryophyllum, and Liriodendron (for details of examples thus quoted refer to Part II.), we are entirely ignorant as to the cause or meaning of the phenomena. In Hedera the leaves of the climbing shoots differ from those of the free flowering shoots, and somewhat similar phenomena occur in other climbers. In water-plants (Chapter III.) the leaves frequently differ in form, but in this case we are able to see some meaning in the *heterophylly*, as the form is largely dependent upon whether the leaf is floating or submerged. Other cases occur in such epiphytes as Platycerium and Polypodium. Still others are seen in young seedlings (see under Germination below), in Berberis, Cephalotus, Dischidia, &c., and in the cases of anisophylly mentioned below.

Many peculiarities of leaf-form are bound up with the necessity for reduction of transpiration in dry climates, &c.; these are dealt with in Chapter III. (Xerophytes, Epiphytes, Shore-plants, Alpine plants); others with the acquisition by the plant of a climbing habit or a water-habit. Others again occur in Insectivorous plants, Myrmecophilous plants, &c. Others are connected with the storage of reserve-materials for hibernation or for vegetative reproduction, as in bulbs, &c., or with the protection of delicate parts as in winter buds, where the *scales* so commonly seen on the outside are leaves which have abandoned their normal functions (and with these their normal structure) to take over the

function of protection and with it a suitable structure. Scale-leaves occur in other positions and may be mere relics or rudimentary organs with no function at all; such are the scales on many plants whose stems have taken over the usual leaf-functions, or in saprophytes or parasites where the changed mode of nutrition has deprived the leaves of their value as organs of assimilation.

The ordinary leaf described above has an upper or *ventral* and a lower or *dorsal* surface ; the internal structure differs on the two surfaces, as we have seen, and such a leaf is termed a *dorsiventral* leaf. It reacts to gravity in a slight degree but is chiefly sensitive to light, and tends to take up during its growth a definite position with regard to the incident light (the *fixed light position*); in temperate climates this is usually a position at right angles to the brightest diffused light falling upon the leaf, *i.e.* an approximately horizontal position. In the tropics this is often departed from in consequence of the extreme brightness of the light causing a too rapid decomposition of the chlorophyll. Frequently leaves are found which exhibit symmetrical internal structure (palisade-tissue and stomata equally on either side) and place their *edges* to the light, *e.g.* Iris, Narthecium, Eucalyptus, &c.; such leaves are termed *isobilateral ;* they may develope in this position or attain it by twisting. Physiologically, the *phyllodes* of Acacia (q.v.), &c. come under this head, and mention may be made here of the curious leaves of Alstroemeria and Bomarea, which are twisted completely round, and may perhaps have gone through an intermediate isobilateral stage. Finally, in some species of Juncus, Allium, &c., the leaf is circular in section, with the tissues evenly distributed all round; it stands erect, and is termed a *centric* leaf. The isobilateral and centric types of leaf offer less surface to radiation and hence are less liable to excessive transpiration by day or excessive cooling at night. Many leaves obtain these advantages, however, and yet retain the chief value of dorsiventral structure, viz. the great amount of assimilation due to the extent of surface exposed to light. This they do by movement. Most Leguminosae execute *sleep*-movements with their leaves at night; the blades (in various ways in different plants) move so as to place their edges instead of their surfaces

upwards. Oxalis is a good example and there are countless others (see Darwin's *Movements of Plants*). In the tropics many leaves execute similar movements in the heat of the day, so that the light shall strike their surfaces obliquely, and thus not cause excessive decomposition of chlorophyll. The hanging of young leaves and shoots (see Chapter III.) is a similar phenomenon. We may also mention the 'compass-plants' Lactuca and Silphium. An exaggeration of the ordinary sleep-movements (which are regulated by the stimuli of light and temperature) is seen in Mimosa, whose leaves take up the sleep position on being touched. Biophytum, Neptunia, &c. exhibit the same phenomenon. Lastly, *Desmodium gyrans* exhibits spontaneous movement without any apparent stimulus at all. The movements in all these cases take place by means of more or less swollen joints or *pulvini*. The pulvinus is chiefly composed of parenchymatous tissue, and the cells on one side gradually (or suddenly in Mimosa, &c.) lose their turgidity under the influence of the stimulus, while those on the other side retain theirs; the result is a bending of the joint. When the flaccid cells regain their water the joint straightens once more.

The acuminate apex so common in tropical leaves is apparently an arrangement for rapidly drying the blade (see Chapter III., Tropical Vegetation). In many plants, *e.g.* Rutaceae, Guttiferae, &c. the leaves show pellucid dots when held up to the light; these are oil cavities in the tissue. Lastly we may mention, as curious and as yet unexplained features the holes in the leaf of Monstera (see also Aponogeton), the pockets of Xanthosoma, the curious blades in Codiaeum, the grooved petioles of Fraxinus, &c.

Like the leaf itself the stipules also show great variety of form; in *Lathyrus Aphaca* they do the assimilating work, whilst the rest of the leaf is transformed into a tendril, and in Azara, Viola, Rubiaceae, &c. they do a great deal of assimilation. Or they may be scaly and aid in bud-protection (below), or be represented by tendrils (Smilax), thorns (Acacia, Paliurus, &c.), hairs (Anacampseros), and so on.

The Stem. The stem is really little more than an apparatus for spreading out the leaves to good advantage as regards light and air. Some plants have very short stems indeed, and by consequence few leaves; others have tall erect

stems; others again have creeping or climbing stems, and so on. If this fact, that the first great function of the stem is to spread out the leaves to advantage, be kept in view, the great variety in stem morphology that is met with presents but little difficulty; the same general object is fulfilled in all cases with reference to the peculiar circumstances of life or growth of the particular plant. The second great function of the stem is to carry, by means of its vascular bundles, materials to and from the leaves, and thirdly, in perennials, it is the most common place for storage of reserve-materials. As in the case of the leaves, so here, other less common functions are at times performed.

Leaving out of consideration for the present the creeping, climbing, and other less common kinds of stem, we shall deal with the ordinary erect stem. The spreading out of the leaves is dependent on various factors—the height of the stem, the branching, and the actual relative positions of the leaves upon the stem (*i.e.* their *phyllotaxy*); it is further aided by the petioles of the leaves. The stem morphology is also affected by the growth in thickness that occurs where there is increase of leaf surface, whether by increased height or by branching of the stem.

Generally speaking, the stem consists of a more or less elongated axis bearing leaves; the points at which these are borne are termed the *nodes*, the intervening spaces the *internodes*. Progressing towards the apex these become shorter and shorter till we find them of microscopic length in the actual apical *bud*, which crowns the tip of the stem.

The Bud. A bud is simply a much-condensed shoot, consisting of a short stem with crowded nodes, at which are borne young leaves. The tip of the stem is covered by the young leaves folded over it; if they be removed (as can easily be done in Hippuris) and the apex of the stem exposed, it is seen under the microscope to consist of a convex mass of embryonic tissue, on which arise, *exogenously* (*i.e.* from the external layers of cells), lateral swellings, in acropetal succession (cf. the development of roots), *i.e.* the youngest nearest the apex and successively older ones further and further back. At first all alike, these outgrowths ultimately differentiate into leaves and branches. Branches thus produced are termed *lateral* branches. Another type

of branching is common in Algae &c., viz. *dichotomy*, where the growing apex divides at the summit into two equal halves, but this type is practically unknown in the higher plants. We shall return to the subject of branching below. The bud is a very important part of the plant, and one which from the young and tender nature of its parts is very susceptible to injury. In tropical climates with plenty of moisture the bud is liable to injury by the intense radiation decomposing its chlorophyll, or by heavy rain damaging the young leaves. In very dry places it is further liable to excessive evaporation. In temperate climates the bud is exposed during the winter to snow, rain and cold. Against all these dangers buds are protected in various ways, by the older leaves, by scale leaves, by hairs &c.; these are dealt with in Chapter III. (see Herbs, Trees, Xerophytes &c.). Buds are often detached bodily from the parent plant to start growth on their own account as independent plants; in these cases of vegetative reproduction (see below) they are usually large, being provided with a store of reserve-materials with which to commence growth. This pheno-menon is widely spread in water-plants (Chapter III.).

The Branches. We have seen that at the growing apex of the stem exogenous outgrowths are formed, some of which usually develope into branches. Comparatively rarely is a stem quite unbranched; if not in the vegetative part, it is usually branched in the inflorescence portion. If however we leave the latter out of account we may say that the stem is unbranched in most Palms and many other Monocotyledons, and in a few Dicotyledons. The branching is lateral, as already mentioned, and commonly the position of the branches bears some definite relationship to that of the leaves. In many ferns the branches appear on the leaf-bases, in Equisetum they are *axillary* (*i.e.* in the angles between leaves and stem), and the same is so generally the case in flowering plants (except Pistia &c.), that the usual mode of deciding whether a doubtful structure is of leaf or stem nature, is by noticing whether it subtends an axil or stands in one itself. In Selaginella and Lycopodium the branching has little relation to the leaves. The number of branches arising close together is usually small and most commonly only one. Other branches

than the usual one, arising in the same place, are called *accessory;* they may be *collateral* (side by side in the same axil) as in species of Acer, Salix, &c., or *serial* (one above the other) as in Calycanthus, Gleditschia, Cercis, Robinia, Colletia, Syringa, Aristolochia, Fuchsia, &c.

The simplicity of the morphology of the stem and its branches is often much interfered with by the phenomena of *adnation.* The branches and leaves originally arise as free and separate outgrowths upon the growing point, and in most cases remain so throughout their development. Often however a growth of the tissue lying beneath two or more of them takes place in such a way as to lift them up upon a portion of shoot common to both or all. The most simple case is where a leaf is 'adnate' to its own axillary shoot, so that the latter appears to spring from the main stem without reference to any leaf. In reality the two started separately, but afterwards the subjacent tissue took part in the growth carrying them both out upon a common prolongation of the main axis. If the normal state of things be represented by the first diagram (the upright line representing the main stem), the condition when adnation occurs may be shown by the second diagram. Since the common tissue is usually stem-like in appearance, the leaf is thus made to look as if it belonged to the branch and not to the original stem. A very common case is that the axillary shoot is 'adnate' for a greater or less distance to the main shoot from which it sprang; *e.g.* in Anthurium and other Araceae, Cyperaceae, Potamogetonaceae (*e.g.* Zostera), Solanaceae, Cuphea, Asclepias, &c. Some of these only show the phenomenon in the inflorescence portion of the shoot.

A very frequent phenomenon is the possession by a plant of branches of two kinds—*long* and *short shoots.* The former grow indefinitely, whereas the latter remain short, often resembling little tufts of leaves. See Coniferae, Pinus, Berberis, Spergula, Cactaceae, &c.

It must not be supposed that all the branch buds formed near the apex of a stem develope at once. In perennial plants at any rate, only a small proportion of them usually do so. The rest remain as *dormant buds,* but may start into active growth if the others are killed or injured. The

branches that appear later in life from the lower parts of stems are sometimes formed from dormant buds, but very often are adventitious, developed from new buds formed without reference to the old leaf-axils. The formation of the flowers not on the young twigs but on old stems, so common in tropical trees, is often due to the presence of dormant buds (see Tropical Vegetation in Chapter III.).

Lateral branching is generally according to one or other of two types, which have special names, the *monopodium* and the *sympodium*. In the former, of which Pinus and many other Conifers are the · best examples, the same growing point continues in a straight line from year to year and forms branches in regular succession, which do not overtop the main axis. This type is very common in herbaceous plants with erect stems. The sympodium is found in most of our forest trees and in many shrubs, herbaceous plants with rhizomes, &c. Here the successive lateral branches in turn overtop and supersede the relatively main axis; the growing point, which for the time being is the main one, is pushed aside by the growth of the branch, which thus comes into line with the axis from which it sprang. The original termination of the old axis is thus made to look like a branch of the straight stem. The second growing point is in turn pushed aside and so on, so that the actual straight stem is formed of a succession of pieces each added by a separate growing point. This may be roughly represented by such a diagram as is here given, each L representing one *limb* of the sympodium, arising as a branch upon the one below it. Very often only one limb is formed each year, and during that period branches monopodially; the last lateral bud then pushing the terminal one aside in the following year. Excellent examples of sympodia are: beech (Fagus), virginian creeper and vine (Vitis), the rhizomes of Iris, Juncus, &c., the flowering shoot of *Geranium pratense*, &c.

The increase of weight to be borne, of leaf surface exposed to the wind, and of transpiration and assimilation, necessitate a corresponding increase in the strength and in the carrying capacity of the stem and so we find that stems, which by branching or otherwise increase their leaf surface, grow steadily in thickness, forming new xylem and

phloem. A very large proportion of the new material in erect stems consists of fibres or strengthening tissue. This process of growth in thickness is rare in Monocotyledons and Pteridophyta, but occurs in a very large proportion of Gymnosperms and Dicotyledons. With the details of the process we are not concerned here.

Phyllotaxy. The arrangement of the leaves upon the stem is not a haphazard matter but is, especially in Angiosperms, according to definite rules; in the same species the arrangement is always (with rare exceptions) the same, though it varies within certain narrow limits. The particular mode of arrangement of the leaves upon the stem is called their *phyllotaxy*.

Leaves may be several at each node, when they are said to be in *whorls*, or two at each node (usually *opposite*) or one (*alternate*). When the stem is so short that the leaves, as in the primrose or dandelion, are all crowded together and spring from the level of the ground, they are said to be '*radical*.' In the first two cases, as a rule, the leaves at one node stand above the gaps between those at the node below (opposite leaves thus arranged are termed *decussate*, *e.g.* most Labiatae). It is only in the case of alternate leaves that we find much variety of arrangement. There is found to be, on examination, a fairly constant angle between each leaf and the next one above it, *e.g.* in wallflower this angle is $\frac{2}{5}$ of the whole circumference (it is always measured the nearest way). This fraction $\frac{2}{5}$ represents the phyllotaxy of the wallflower. A little consideration will show that (twisting of the stem excepted) the leaves will stand in 5 vertical rows, each divided from the next by $\frac{1}{5}$ of the circumference. For if we start from any leaf 1 and pass by the nearest way through all consecutive leaves till we come to leaf 6, this must be above 1 again. Leaf 2 will be $\frac{2}{5}$, 3 will be $\frac{4}{5}$, 4 will be $\frac{6}{5}$, 5 will be $\frac{8}{5}$, and 6 will be $\frac{10}{5}$ of the circumference from leaf 1, *i.e.* immediately over it, and two turns of the spiral above it. Hence the rule for determining phyllotaxy: start from any leaf A and draw a spiral round the stem, passing by the nearest way through all consecutive leaves, till you come to the leaf B exactly above the leaf A; then the number of leaves from A to B is the denominator, the number of turns of the spiral the numerator, of the fraction representing the phyllotaxy.

Gramineae have the phyllotaxy $\frac{1}{2}$, *i.e.* leaves alternately on opposite sides of the stem. Cyperaceae have $\frac{1}{3}$ phyllotaxy. A curious point is that nearly all other actual arrangements are terms of the continued fraction starting from $\frac{1}{2}$, $\frac{1}{3}$. If we add the numerators together to make a new numerator, and treat the denominators in the same way, we get the next arrangement $\frac{2}{5}$. This with $\frac{1}{3}$ gives the next, viz. $\frac{3}{8}$, and then we get $\frac{5}{13}$ and so on. It is rare however to find a stem that shows the phyllotaxy very clearly, for usually in the course of growth more or less twisting occurs. The advantage of the phyllotaxy is that the leaves are spread out so as to occupy the available space to best advantage; the larger the number of vertical ranks the better is this effected, and the less shading of the leaves by one another will there be. [For further details of phyllotaxy reference should be made to Asa Gray's *Structural Botany*; for an account of its influence on Botany generally, see Sachs' *History of Botany*, book I. chap. IV., and for the newer developments and mechanical theory, see Schumann's *Morphologische Studien.*]

The advantageous spreading out of the leaves is further assisted by the formation of petioles or leaf-stalks which carry the blades away from the stem and thus of course increase the space available. The stalk is further of advantage to the leaf by enabling it to move more readily in the direction of the wind, so that the risk of tearing is much lessened. A large leaf is never without a petiole, although small ones are commonly sessile.

An examination from above, of a branch, say of a Horse chestnut (Aesculus), shows that the leaves, owing to the various lengths of stalk and other points, are very well arranged so that there is but little shading of one another, and that there is hardly any space unoccupied. They form what has been termed a *leaf-mosaic.* Such mosaics are common in plants of our climate and deserve more attention than they have hitherto received. See Kerner's *Nat. History of Plants*, Vol. I., or Lubbock's *Flowers, Fruits and Leaves.*

Care must be taken to avoid the error of supposing (as its discoverers supposed) that phyllotaxy is a very clearly defined phenomenon; in small plants there is not generally much deviation from the 'rules,' but in shrubs, trees &c. there are often several different arrangements of the leaves

on one plant. With branches spreading in every direction, it is easy to see that a strict adherence throughout, say to the $\frac{2}{5}$ phyllotaxy, would lead to considerable disadvantages, when we remember the principle upon which the leaves take up their position with regard to light. We usually find, in fact, that the branches, if standing out more or less horizontally, exhibit a symmetry different from that of the main erect stem, and this difference depends as a rule upon the possession of a different phyllotaxy. In most cases the branches, if horizontal or nearly so, exhibit a *dorsiventral symmetry*, contrasting with the usually *radial symmetry* of the main stem. In the latter the leaves are equally arranged all round, whilst in the former they are arranged at two sides, with their surfaces more or less in the horizontal plane. This may be effected by a twisting of the leaves from the various positions in which they arose, but is usually considerably aided by the possession of a two-ranked phyllo-taxy, the leaves arising upon the sides of the axis, and merely having to twist at their bases to place themselves horizontally. A further consequence of this is that the axillary branches also stand much in one plane. Good examples of this may be seen in the elm (Ulmus), yew (Taxus), lime (Tilia), Betulaceae &c. See also Abies, Pinus, Anona, &c. In branches thus obliquely placed, a very common phenomenon, termed *anisophylly*, may often be observed. The leaves which are borne on the under side of the branch are larger than those on the upper, while the lateral leaves occupy an intermediate position in this respect. The difference is especially well seen in plants with opposite leaves. The phenomenon is largely dependent on external stimuli— gravity, light &c.—but is hereditary or *habitual* in a number of plants. As examples of anisophylly may be mentioned Centradenia, many Melastomaceae, Strobilanthes, Columnea, Tabernaemontana, Gardenia, Philadelphus, Salvia, Sambu-cus, Ligustrum, &c. The phenomenon is one of the many that fall to be considered under the general heading of symmetry in plants, about which we as yet know very little. For further details, see Wiesner's *Anisomorphie der Pflanze* in Sitzb. k. Akad. Wien, CI. 1892, and *Studien ü. d. Aniso-phyllie tropischer Gewächse*, loc. cit. CIII. 1894.

In other plants, again, alterations of phyllotaxy occur for

which no explanation can at present be given; *e.g.* in Sola-
naceae, Cynocrambe, Quisqualis, Eucalyptus, Baptisia &c.

Another cause that interferes with the simplicity of
phyllotaxy is the twisting of the stem that occurs in many
cases. Pandanus shows it as a regular case, whilst it is
frequent in grasses and many other herbaceous plants. [See
De Vries in Pringsheim's *Jahrb. für wiss. Bot.*, Vol. XXIII.]

With the *habit* (external appearance and general im-
pression) of the stem we shall deal in Chapter III. There
are a number of descriptive terms applied to stems, however,
which are best given here.

[*Technical terms applied to Stems.* Most of these explain themselves.
The stem may be *herbaceous* (not woody in any part above ground),
*woody, solid, hollow, succulent; erect, prostrate, twining, creeping,
climbing, floating* &c.; *cylindrical, angular, ribbed, winged* &c.; *smooth,
prickly, hairy* &c.; *branched* or *unbranched.* Other terms, applied to
less common types of stem, are mentioned below.]

The performance of the second great function of the
stem—carriage of material to and from the leaves—is effected
by the vascular bundles; as the leaves increase in number
the stem grows in thickness, but otherwise the performance
of this function does not materially affect the external mor-
phology of the stem.

As with the rest of the plant, the living cells of the stem
need to respire; so long as the stem is green it has stomata
in the epidermis, but as it grows in thickness bark (cork) is
formed, and this tissue is practically water- and air-tight. To
provide for respiration special organs (*lenticels*) are formed
in the bark; these are portions of bark in which the cork
cells are loose and powdery so that air can pass between them.
They appear upon the surface of the bark as little eruptive
craters full of a brown powder; they are specially well seen
in Elder (Sambucus) but are easily distinguished upon any
young twig.

Storage of reserve-materials in perennial plants is a func-
tion very commonly undertaken by the stem, and one which
is often much in evidence in the external morphology. In
woody plants the materials for subsequent growth are usually
stored in the wood of the stem, and only rarely does storage
take place to such an extent as to necessitate extra growth

in thickness beyond that necessary for the performance of the functions already dealt with. Cases in which extra growth in thickness, only explicable as necessary for increased storage, regularly occurs, are found in Bombacaceae, Jatropha sp., &c. Herbaceous stems above ground are not usually suited to storage purposes, though some cases occur (succulent stems of Xerophytes, see Chapter III.), as they die down in winter (or the dry season in warm countries) and here storage is usually found below ground, in such peculiar shoots as bulbs, corms, rhizomes, tubers, &c. These are dealt with in Chapter III. (Herbs, Xerophytes, &c.). Such stems also lend themselves readily to vegetative reproduction (see below).

Other types of stem are found in water-plants, climbing plants, xerophytes, epiphytes, &c. (see Chapter III.). These are mostly explainable by the necessity for modification of the structure bound up with that for modification of certain functions due to different climate or situation.

Growth and Movement of Shoots. The growth of a shoot, like that of other parts, takes place only under suitable conditions, viz. (1) a supply of material to the growing parts, (2) a supply of energy to build up new protoplasm, &c., (3) an adequate temperature, and (4) in most cases, a supply of sufficient water to the growing parts to maintain the cells in a condition of great turgidity (see text-books of Physiology). The supply of material is brought from the leaves or from storage places; the energy is obtained from the breaking-down of protoplasm, &c. into simpler products (this is exemplified by the fact that growth will not go on in absence of oxygen, and by the very vigorous respiration characteristic of growing organs); that an adequate temperature is necessary is a familiar annual experience in temperate countries; and that turgidity is needful is easily proved by simple experiments, and indicated by the fact that a plant will not grow unless well supplied with water.

The rapidity of growth is dependent upon various factors, some external, some internal to the plant itself. Light retards growth, as is proved by actual measurement of the rate of growth of the same plant during day and night, and as is also evidenced by the phenomena of *etiolation* (growth of green plants in darkness; under these circumstances the

stems grow very rapidly, but are very slender, the internodes being long, the leaves small ; chlorophyll is not developed, but rather a yellow colouring matter termed etiolin). Below a certain temperature (varying according to the plant and the climate) growth will not take place. As the temperature rises from this minimum, the rate of growth increases, till it reaches its maximum at a temperature which is termed the optimum temperature for growth in that plant ; as the temperature rises beyond this, growth decreases, till a maximum temperature is reached, beyond which growth will no longer go on. [It may be noted here that all plant functions exhibit similar relations to the temperature.] The rate of growth is also affected by conditions internal to the plant, especially the amount of food supply and the rapidity with which it is made available. The growth of seedlings or of buds opening in spring is usually more rapid than that of parts which have not the advantage of a rush of food from some reserve store, but depend upon that provided from day to day by the leaves. The direction of growth of the shoot, as of the root, is also influenced by external stimuli. If left to itself without any external stimulus, the tip of the shoot would grow straight forward, though as a rule *nutating* as it did so. By this is meant that the apex moves alternately from side to side or round a circular or elliptical orbit ; the phenomenon is due to varying rate of growth of the cells a little way behind the tip. As the growth of the cells becomes complete, however, the shoot assumes the straight line. If the shoot be exposed on one side more than the other to the stimulus of light or gravity, it executes, in its growing portion, movements tending to do away with the irregular distribution of the stimulant action. Thus an ordinary erect stem tends to grow straight upwards under the action of light and gravity, being negatively geotropic and positively heliotropic. Creeping stems on the other hand place themselves at right angles to the stimulus, *i.e.* are *dia-heliotropic* or *dia-geotropic*. As in the case of the roots, the lateral branches commonly react in a different way from the main stems. Sensitiveness to contact stimulus is found in some stems, but almost solely in climbing plants, and there more especially in tendrils (see Chapter III.).

Reproductive Organs.

The chief feature in the life-history of a plant is its reproduction, and it should always be borne in mind that the preservation of the individual is of far less importance than the preservation of the species ; in fact we may almost say that the former is only of importance in so far as it affects the latter.

It is very customary to divide the methods of reproduction into two—*vegetative* reproduction, and *true* reproduction. By the former is understood reproduction by the detachment of portions of the vegetative system—specialised for the purpose or not—which may grow into new plants without any further reproductive phenomena. By 'true' reproduction, on the other hand, is understood propagation by special *cells* set apart for the purpose. These cells may be able to form new organisms without any sexual process, or they may require, as a preliminary to further growth, to fuse together (or portions of them) in pairs, male and female. In the first case we speak of asexual reproductive cells, or *spores*, in the second of sexual reproductive cells, or *gametes*, which by their union produce a new cell, the *zygote*, which is capable of further development into a new individual.

We have seen above that in those plants with which this book deals, these two latter methods of reproduction occur alternately in the life cycle. We shall deal first with true reproduction, and then with vegetative. Before proceeding, however, to the consideration of the morphology of the reproductive organs, we must discuss certain general features a little more in detail.

Fertilisation. This consists essentially in the coalescence of a male nucleus (and probably some of the cell-protoplasm too) with a female cell or nucleus. In the three lowest groups of plants (the Thallo-, Bryo-, Pterido-phyta) the most common case (and in the two latter the only one) is that the female cell or *ovum* is enclosed in a cavity, often flask-shaped, the *oogonium* or *archegonium*, whereas the male cell (*antherozoid* or better *spermatozoid*) is motile, having no cell-wall when mature, and swimming by means

of *cilia* or moveable threads of protoplasm. This of course implies water to swim in. Most of the Algae and many Bryo- and Pterido-phyta are water-plants, and in the others the sexual cells are produced near or upon the soil, and in places where there is at times enough water for the purpose. The question arises, how does the male cell ever find the female? Pfeffer showed that from the mucilage in the neck of the archegonium there diffuses a substance possessing an attraction for the spermatozoids (in ferns it is malic acid). These are sensitive to the chemical stimulus and swim from places of weaker to places of stronger concentration of the attractive body; thus in nature they find their way towards and into the archegonium, where the fusion takes place. This sensitiveness to chemical stimulus is termed *chemotaxis.*

In the highest group of plants, the Spermaphyta or Phanerogams, we no longer find a free swimming male cell, and fertilisation no longer occurs, except sometimes indirectly, by water agency; the gametophyte is enclosed in and dependent on the sporophyte, and occurs in the flowers, frequently far removed from the ground. The ovum is no longer freely exposed to the outer air, but is sunk in the ovule, and this latter again, in Angiosperms, in the ovary. The microspores, which in Pteridophytes fall upon the soil and produce a male prothallus and spermatozoids, here appear as pollen grains, and the first stage towards the process of fertilisation consists in the transport of these grains, by wind, water, or other agency, to a certain part of the ovule or (in Angiosperms) ovary where their further development takes place. A *pollen tube* is formed from the grain when the conditions are favourable, and at its tip the male nucleus, &c., travel downwards towards the ovum and at length fertilisation takes place. In Gymnosperms the ovule is not enclosed in an ovary and the pollen grain comes to rest on its apex; the tube burrows through the tissue of the ovule to the ovum. In Angiosperms the ovule is enclosed in the carpel or ovary, whose receptive part, usually the tip, is the *stigma*, frequently secreting a sticky sugary fluid. In this the pollen grain germinates and the tube enters the stigma and burrows down towards the ovules. Two possible ways of reaching the ovum are open

to it. It may burrow to the stalk of an ovule and up through the ovule itself, or may enter the ovary cavity, pass to an ovule, and enter at its apex (*micropyle*). In the former case the fertilisation is said to be *chalazogamic*, in the latter *porogamic*. Chalazogamy was discovered by Treub in Casuarina, and afterwards in Betula, Alnus, Corylus, Carpinus and Juglans by Nawaschin and Miss Benson (see Chalazogamae in Part II.). All other seed-plants so far as yet known are porogamic.

As might be expected from analogy, chemotaxis is of importance in guiding the pollen tube. The stigma contains a substance (usually, it would seem, sugar) attractive to the tubes, and their entrance into the stigma is thus guided. The same substance occurs in the style but in less strength and is therefore useless for further guidance, the tubes making their way simply by the mechanical guidance of the harder tissues which surround the soft part or even open space in which the tubes grow. Approaching the ovule, chemotaxis is again brought to bear, a secretion emanating from the micropyle and guiding the tube in.

The result of successful fertilisation in Phanerogams is the formation of a seed which grows into a new asexual plant.

Cross- and Self-Fertilisation. A consideration of the observations on inbreeding &c. in animals soon led to the question whether anything similar was to be found in plants. If, of the ova of plant A, some be fertilised by male cells of A, some by male cells of a different plant of the same kind, B, will there be any difference between the offspring of self-fertilisation (A × A) and that of cross-fertilisation (B × A)? The answer to this question is supplied by the experiments of Darwin, detailed in *Cross- and Self-Fertilisation of Plants*, and supplemented by those of Miss Bateson (*Annals of Bot.*, Vol. II.) and others. Starting in each species with a plant A, seeds were obtained by self-fertilisation (AA) and by fertilisation with pollen from a distinct plant (BA). These were planted in pairs, one of each kind, in pots, and thus brought into competition. Then when fully grown, the heights and weights were measured, and the number and weight of seed produced. AA were again self-fertilised (AAA̅), BA again crossed (CB̅A̅), and the new offspring

similarly treated for a number of years. The results were surprising. Even in one generation the offspring of cross-were superior in height, weight and fertility to the offspring of self-fertilisation; only a few exceptions occurred, but it is important to note that they did occur. In the succeeding generations the result became more and more marked, and after several years was frequently of the most remarkable kind. We may thus conclude, not, as has been so often done, that self-fertilisation is necessarily or in itself harmful, but that in general, *the offspring of cross-fertilisation will vanquish that of self-fertilisation in the struggle for existence, if the two be brought into direct competition,* other things being equal. It is of importance to remember that the advantage due to crossing is compounded of several factors which, as Darwin's results show, do not enter into the product in equal degrees; in fact as a rule if the gain in one of the three chiefly measured by him (fertility of the parent plant; strength of constitution of the offspring; fertility of the offspring) be very great, there is usually little or none in the other directions. Besides the advantages thus measured, it is very probable that a gain is made in the increased variability of the offspring resulting from cross-fertilisation, but we are too ignorant of variation and evolution to dogmatise.

On the other hand as compared with self-fertilisation crossing has certain drawbacks. It is (1) much less easy to ensure fertilisation when the pollen has to come from a distinct plant, and (2) fertilisation tends to be delayed (a point of importance in the short summer of alpine and arctic regions, where seed must be ripened before winter).

The advantages of cross-fertilisation are often great, and frequently enormous, and as at the first glance they appear to be obtained at little or no cost, we are inclined to expect this method of propagation to prove almost universal. The earlier workers at this subject in fact set out with the idea that cross-fertilisation was so to speak the primary object of a flower's existence, whilst self-fertilisation was actually harmful.

The well-known Knight-Darwin hypothesis, " that no organic being fertilises itself for an indefinite number of generations, but that a cross with another individual is occa-

sionally, perhaps at long intervals, indispensable," is the outcome and expression of the work of this period. Then Müller showed how common self-fertilisation is, and proposed to give up the Knight-Darwin hypothesis as a basis for the study of fertilisation phenomena, substituting for it the simple statement based on Darwin's experiments that " the offspring of cross- vanquish the offspring of self-fertilisation in the struggle for existence." This statement certainly fits the facts better than the first, but MacLeod has shown that it too will have to be given up in so far as it aims at representing the underlying principle in the variety of fertilisation phenomena that exist. Self-fertilisation is common and is certainly the rule in many plants, although as the flowers are open there is a remote chance of a cross, but in Myrmecodia, &c. Burck has found crossing absolutely prevented, the flowers never opening. Hence the Knight-Darwin hypothesis must be abandoned.

An important conclusion easily drawn from the facts of the case is that cross-fertilisation costs the plant a certain price. If self-fertilisation be the rule, there is no necessity for any further complexity of flower beyond the organs bearing pollen grains and ovules (*i.e.* stamens and carpels), except something to ensure that the pollen shall reach the stigma, and that the pollen shall be protected from injury by rain, &c. No more pollen than what is absolutely necessary for fertilisation need be produced. If, however, the flower is to be crossed, extra expenditure must be made. If the carrying agent for pollen be wind or water, a vast amount of pollen must be wasted; if it be insects, though there is less waste, there must be brightly-coloured organs, scent, honey, &c., to attract them. Thus it is that *the plant has to pay a certain price for its cross-fertilisation* (this price being affected by many factors as we shall afterwards see), and *only when the gain resulting from crossing is greater than the price to be paid for it, will cross-fertilisation prove an advantage to the plant.* If the gain ceases to exceed the price, then if the plant is capable of varying in the direction of self-fertilisation, it will probably do so, if not, it may gradually die out, as seems to be the case with some plants at the present day.

The theory we have thus briefly sketched is due to

MacLeod (see his paper in *Botanisch Jaarboek*, Gent, v. 1893, also *Science Progress*, Nov. 1895; the history of the subject will be found in the former, and in Müller's *Fertilisation of Flowers*; see also Sachs' *History of Botany*).

The advantages of fertilisation seem to rest upon the fact of the two parents having grown under slightly different conditions of life. The effect of a cross between two separate flowers on a plant A is but little if any better than that of the purest self-fertilisation within one flower, and the good effect of a cross A × B is greater if A and B have been grown at a distance apart than if grown near together. This is expressed in Nägeli's law that "the consequences of fertilisation reach their optimum when a certain mean difference in the origin of the sexual cells is attained." Varieties are frequently even more fertile together than plants of the same form, but when we go further and cross different species the value of fertilisation decreases again, sterility becoming a more or less marked feature in such unions.

The Organs of Reproduction. There is good reason for believing, as we have already seen, that the differentiation of the reproductive and vegetative functions took place at a time previous to that at which the differentiation of the vegetative functions from one another occurred; hence it is evident that we must be careful in comparing the organs of reproduction with the vegetative organs. We have no right to say, for example, that a sporophyll is a modified vegetative leaf; perhaps we should be more near the truth if we said that a vegetative leaf was a modified sporophyll, for we have seen that the sporophyte was reproductive before it was vegetative. It is convenient and justifiable to speak of the sporophylls as the leaves of the reproductive shoot, as their mode of arrangement, development, &c., correspond closely with those of the leaves of the vegetative shoot. We must however beware of assuming, as most text-books of morphology assume, that all the structural phenomena of the reproductive shoot must necessarily have their counterparts in the vegetative shoot.

The essential reproductive organs of the sporophyte— the 'plant' in those forms with which we have here to deal—are the *sporangia* or spore-containing capsules. The

spores may be of one kind or of two. In the former case (Filicinae with exception of the Salviniaceae and Marsiliaceae, Equisetum, Lycopodinae except Selaginella and Isoetes) the plant is said to be *homosporous;* the spores are very small and numerous, and each gives rise to a hermaphrodite prothallus (except in Equisetum and some ferns). In the latter case (all other Pteridophyta and all Spermaphyta) the plant is *heterosporous;* the small and numerous *microspores* give rise to male, the few large *macro-* or *megaspores* to female, prothalli. The two kinds of spores are contained in corresponding sporangia; in the lowest forms these often occur together on one leaf, but in the higher forms of plants they are usually on different leaves.

In the ferns proper, as we have already mentioned, the sporophylls are not usually differentiated from the foliage-leaves; the same leaf usually assimilates and bears the (homosporous) sporangia upon its lower surface. In the higher Pteridophytes there is a differentiation of the reproductive part of the shoot (inflorescence or strobilus) from the rest, and the same is the case in the Spermaphyta. In Equisetum there is a cone of sporophylls, all of one kind, and in Lycopodium the same, while in Selaginella the cone consists of micro- and mega-sporophylls. The same is the case in the Gymnosperms and Angiosperms (stamens and carpels corresponding to micro- and mega-sporophylls). If we apply the term flower or inflorescence to the cones of Gymnosperms, we cannot refuse it to those of Selaginella, &c.

The micro- and mega-sporangia of the Pteridophytes are represented in Phanerogams by pollen-sacs and ovules respectively (see articles on these groups in Part II.).

We have studied the morphology of the vegetative organs by tracing their gradual differentiation and specialisation, in the light of the principle of ' physiological division of labour,' and we shall now deal in the same way with the reproductive shoot.

The Inflorescence. In the cones of Lycopodinae, Equisetinae, and Gymnosperms we see simply an axis bearing an indefinite number of sporophylls, of one or two kinds. This is the most primitive type of reproductive shoot in existence, and we can hardly call it a flower, but

it is no great stretch of a term to apply to it the name *inflorescence*, as we have already done. In these repre-sentatives of early forms there is no differentiation of the inflorescence into flowers such as we see in the Angiosperms, and we do not know how the differentiation took place. The important fact for us however is, that the reproductive shoot or inflorescence is usually differentiated into, or is composed of, or bears, a number of shoots of limited growth (short shoots, p. 34) termed *flowers*. It may be that from each of the numerous cones of the primitive forms one flower was derived, and that the flowers tended to become aggregated together, or it may be that from each cone a number of flowers were derived (see Coniferae in Pt. II.); we have at present no means of drawing a definite conclu-sion, but it would seem probable that the former view is nearer to the truth, for, as we shall see, one of the general phenomena manifested in the upward evolution of flowers is the gradual reduction in number of the sporophylls, and this is more easily harmonised with the assumption that the flower was derived from an entire cone.

It must not be supposed that a plant has only one inflorescence ; very commonly indeed this is so, but most often the reproductive shoots are several in number, divided from one another by portions of the vegetative shoot.

The construction of the inflorescence depends chiefly upon the mode of branching which it exhibits, whether monopodial or sympodial (p. 35), but it is also modified by other phenomena, such as varying rate of growth of its different parts, variation in symmetry, adnation, &c.

The typical monopodial inflorescence is the *raceme*, in which the main shoot grows steadily onwards, bearing lateral branches in acropetal succession ; each branch ter-minates in a flower. The oldest flowers are thus those furthest away from the apex of the main shoot, and the order of opening of the flowers is *centripetal*. This inflo-rescence is also frequently called *indefinite* or *indeterminate*, because the first axis does not, as a rule, end in a flower ; exceptions occur however in Aconitum and other Ranun-culaceae, &c. Good examples of the simple raceme occur in Ribes, Cruciferae, Berberis, Prunus sp., &c. If instead of each branch bearing but a single flower, it bear another

raceme, we get a compound raceme or *panicle*, as seen in oats and many other grasses; the terms applied to inflorescences are, however, very loosely used, and the name panicle is given to any inflorescence presenting this loosely branched appearance, whether the branching be racemose or cymose, or both. If in the simple raceme the flowers be imagined all sessile, we get the simple *spike*, as in plantain. This also may be compounded; true compound spikes occur in wheat and other grasses, &c.; often, however, the secondary branching is cymose. In practice the name spike is given to all elongated inflorescences of sessile flowers, whatever the branching. A variety of the spike is the *catkin*, or pendulous spike, seen in hazel, oak, chestnut, &c. If we imagine the stalks of all the lateral flowers of a raceme to grow as fast as the main axis, we get a simple *corymb*, with all the flowers at one level, as seen in candytuft (Iberis) and other Cruciferae. The name is also given to all branched inflorescences whose flowers stand at about the same level. If we imagine the corymb to have its main axis 'condensed' so that all the stalks of the individual flowers spring from one point—its summit—we get the *umbel*. This is usually compound, as seen in Umbelliferae, and may be cymose (see below). Lastly, if the flowers of the umbel be imagined sessile, the summit of the stalk being enlarged into a *common receptacle* to bear them, we get the *head* or *capitulum*, as seen in Compositae; this too may be compound, as in Echinops, &c.

Before passing on to the sympodial inflorescences, we must consider a few general features.

Each flower arises, as a rule, in the axil of a leaf, which is termed its *bract;* any leaves on the same axis as the flower itself, between it and its bract, are termed the *bracteoles* of the flower.

These terms merely express the relative positions of the parts; the same leaf may obviously be the bracteole of one flower and the bract of another (but as a rule only in cymose inflorescences). Bracts are absent in a few cases, *e.g.* in most Cruciferae, many Umbelliferae and Compositae; the bracteoles also are frequently missing. In Dicotyledons there are usually two bracteoles, placed transversely (*i.e.* if the bract face S. they face E. and W.), in Monocotyledons commonly

one, on the side opposite to the bract   In condensed
inflorescences the bracts are often collected together into
whorls or what look like them, such an aggregation is
termed an *involucre* and may be seen on the heads of Com-
positae, &c, the umbels of many Umbelliferae, and so on
The term involucre is also given to a whorl of leaves below
a single flower and upon the same axis, as in Anemone and
its allies

In general the bracts resemble the foliage-leaves proper,
but they are usually smaller and more simple in con-
struction (*i e* less branched, &c)   In some cases, *e g*
Euphorbia sp, Salvia sp, Castilleja, Amherstia, Bougain
villea, &c, they are brightly coloured, aiding in the attraction
of insects to the flowers   They may also exhibit modification
into thorns, &c, just as the foliage leaves proper do

In many Monocotyledons, *e g* Palms, Araceae, &c, there
is a large leaf borne at the base of the inflorescence and on
the same axis, this is termed the *spathe* and usually encloses
the whole inflorescence when young, the latter, if of the spike
pattern, is then usually termed a *spadix*   The spathe is
brightly coloured in many Araceae, *e g* Anthurium, Zan-
tedeschia

Turning now to the sympodial or *cymose* inflorescences,
the general principle underlying all their variety we find to
be that each branch, when formed, ends in a flower after
bearing a few leaves (bracteoles), usually one or two in
number   From the axils of these leaves the branching is
continued   The term *definite* or *determinate* is often applied
to inflorescences of this type, to indicate this peculiarity of
the branching   The inflorescence (termed generally a *cyme*)
is built up of a number of 'short shoots,' which frequently
form a true straight sympodium (p 35), especially in the
older (fruiting) part of the inflorescence   If each successive
branch bear upon itself one new branch only, the cyme is
termed *monochasial,* if two, *dichasial,* if more, *pleiochasial*
Typical dichasial cymes occur in Caryophyllaceae, Gentian
aceae, &c (A in figure), they are usually found with opposite
leaves, but sometimes with alternate   From the axils of the
bracteoles b_2 of the flower 1 spring shoots, each bearing
two bracteoles (b_3) and a flower (2), and so on. Commonly,
of the two shoots one is more strongly developed than the

other, and the difference often becomes more strongly marked at each branching, and the cyme may thus even become monochasial in its later formed parts (by preference, as it is termed, of one or other bracteole). The figure represents all the shoots in one plane, but usually the plane of each successive pair of branches is at right angles to that of the preceding pair; in other words, the plane of the shoots 3, 3, 3, is at right angles to the plane of the paper.

Monochasial cymes are of four types, the ground-plans of which are represented in the figure. If each successive
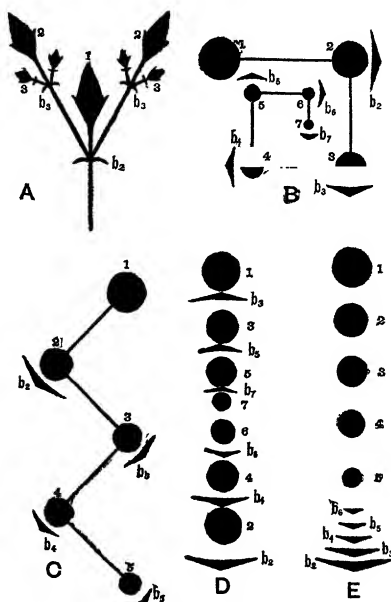
Diagrams of cymose inflorescences (partly after Eichler, but modified). A, dichasial cyme; B, bostryx; C, cincinnus; D, rhipidium; E, drepanium. The figures 1, 2, 3 &c. mark the flowers and their order of age (also indicated by the size of the circles); the letters b_2, b_3 &c. mark the bracts in whose axils the flowers 2, 3, &c. respectively arise. A is a side view, all the shoots being represented in one plane; the rest are ground-plans.

lateral branch fall upon the same side of the relatively main axis, we get the two cases represented by B and E; the former is termed a *bostryx* (Schraubel), and is found in Hemerocallis, Hypericum, &c.; the latter is termed a *drepanium* (Sichel), and occurs in Juncaceae, &c. If each successive lateral branch fall in turn on one side and on the other of the relatively main axis, we get the cases represented by C and D. The former is termed a *cincinnus* (Wickel); it occurs in Helianthemum, Boraginaceae, Hydrophyllaceae, Pentaphragma, Tradescantia, &c., and is coiled up in the bud like a crosier. The latter is similar but has all the flowers in one plane instead of two; it is termed a *rhipidium* (Fächel) and is found in Iris, &c.[1]

Most monochasial inflorescences straighten out more or less into sympodia, which have the appearance of racemes, but are distinguished by the fact that the apparent lateral branches of the raceme are not in the axils of the leaves, but spring from the stem apparently without any relation to these organs.

Whilst an immense proportion of the flowering plants possess inflorescences of the types we have described, a considerable number possess *mixed* inflorescences, in which some of the branchings are cymose, some racemose. For example, in Aesculus the primary branching is racemose, but the lateral shoots each form a cincinnus (this inflorescence is usually termed a panicle; see above). In Labiatae the primary branching is racemose, the lateral shoots however are dichasial. Other examples are Betulaceae, Verbascum, Morina, Ceratostigma. In Statice the primary branching is racemose, but the lateral shoots are drepania. In Haemanthus and many other Amaryllidaceae the apparent umbel is really made up of condensed bostryx-cymes. In Allium and others the condensation is greater and cymose heads are formed. Some species of Juncus have heads of drepania, and so on. Many Umbelliferae have cymose heads or umbels, also Sparmannia, Armeria, Dipsaceae, &c.

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[1] The terms scorpioid cyme and helicoid cyme are avoided, on account of the hopeless confusion of their definitions in the various text-books. The student should familiarise himself with these forms of cymes by constructing models out of matches with sharpened lower ends (the head representing the flower).

These inflorescences are distinguished from true heads, &c., by the fact that the order of opening of the flowers is not centripetal.

The simplicity of the morphology of the inflorescence is interfered with by phenomena of adnation (p. 34) even more often than that of the vegetative shoot. Reference should be made to Solanaceae, Samolus, Cuphea, Tilia, Erythrochiton, Chailletia, Spathicarpa, Spathiphyllum, &c.

Another frequent case is the *reduction* of a complex inflorescence to a simple one by abortion of its flowers during its evolution. Thus the umbels of Xanthosia and Chorizanthe, the dichasia of Mirabilis, the heads of Echinops, are each one-flowered; the female head of Xanthium two-flowered. In these cases comparison with the related forms, and the frequent possession of an involucre by the one flower, leaves no doubt as to the explanation. An immense number of plants have true *solitary* flowers, *i.e.* usually one flower in each leaf-axil, loosely arranged on the main axis. These *may* be reduced inflorescences but in most cases, probably, are not so. One of the most interesting cases of reduction is the cyathium of Euphorbia (*q.v.*), in which a whole inflorescence is reduced in such a way as to look like a single flower, whilst really composed of many individual flowers. This inflorescence has separate male and female flowers, arranged in a definite way with regard to one another; similar phenomena are observed in many Moraceae (*e.g.* Brosimum), Begonia, Echinophora, Ficus, Cyclanthus, &c. All these last-mentioned plants have inflorescences of peculiar types, and reference should be made to Part II. for details; see also Urticaceae, Triumfetta, Spiranthes, &c.

In Acroglochin, Rhus, &c., many of the twigs of the inflorescence do not end in flowers and may be afterwards used in aiding seed-dispersal.

Before leaving the subject we must briefly consider the natural history of the inflorescence. One great advantage, underlying the differentiation of the shoot into vegetative and reproductive parts, seems to be the formation of many spores near together on the shoot. In Cryptogams this is useful because the prothalli also will tend to be nearer together upon the soil, thus favouring fertilisation. In

Phanerogams the microspores (pollen) have to be carried to the ovules or carpels; this generally happens by the aid of wind or insects. In either case the massing together of the flowers tends to free them from the vegetative leaves, which interfere with wind-transport by interposing obstacles, and with insect-transport by rendering the flowers less conspicuous. In insect-fertilised flowers the further evolution of the inflorescence has chiefly gone on. The more the flowers are massed together the more conspicuous do they become, and the more quickly can they be visited by insects. Further, a reduction in the size of the individual flower may be made. The highest degree of perfection in this way is found in the Compositae (*q.v.*). Further conspicuousness is often gained in other ways, *e.g.* by ray flowers, as in Compositae, &c., coloured bracts (see above), unilateral arrangement of the flowers (Digitalis, Mitella, Boraginaceae, &c.), and so on.

The Flower. We have seen that the flower may be defined as a reproductive short shoot. It consists essentially of an axis (*receptacle* or *torus*) bearing sporophylls (*stamens* and *carpels*). We shall deal with the morphology from an evolutionary and biological point of view, as we have dealt with that of the vegetative organs, endeavouring to trace the gradual upward evolution and differentiation of the various parts in the light of the principle of the physiological division of labour. It is necessary to keep clearly in mind what has been said above about cross- and self-fertilisation. The primary object of the flower, to speak in a figurative manner, is to set seed with as much economy of material as possible. All saving of material in the flower may be applied to increasing the weight or number of the seeds (see below). Cross-fertilisation brings such benefits in its train that a great number of plants find it worth while to pay for it, and this introduces numerous complications into their morphology. Others again have, in the course of ages, gone back once more to self-fertilisation, but the adaptations for crossing may still remain in a more or less imperfect condition. Another important point is the protection of the pollen from the weather; this is attended to in a variety of ways. Economy of pollen is another feature, and one which largely explains the advantages of irregularity

and other peculiar morphological constructions. Complex though the morphology of the flower be, it can be very largely explained in the light of the above general principles. *How* the evolution took place is of course another matter; the important thing for us at present is that it did take place, and probably along certain lines which we can without much difficulty picture to ourselves.

We are met at the outset by one of the chief difficulties; we do not know anything about the transition from the seedless Pteridophyte, whose spores fell out of their sporangia and germinated upon the soil, to the seed-bearing plants, in which the megaspore (embryo-sac) remained enclosed in the sporangium (ovule) and germinated there. The gametophyte during this period of transition became parasitic upon the sporophyte (cf. the transition from Bryophytes to Pteridophytes, p. 17). Again, we do not know whether the early cone inflorescences each represent a flower or whether each differentiated into several flowers. We may however accept the former view as quite probable and picture to ourselves the earliest flowers as cones of sporophylls. Those of Coniferae (*q.v.*) may serve as an illustration. We do not know, again, if all the sporophylls in any flower bore the same kind of sporangia, or whether some bore micro-, some mega-, sporangia. Selaginella has mixed cones, the Coniferae have not. Most Angiosperms now existing have mixed flowers, with both stamens and carpels. [Such a flower is termed *hermaphrodite*, whilst one with stamens only is *male*, with carpels only, *female*. These terms are of course not strictly accurate when regard is paid to the alternation of generations, but they are convenient and well-established. When the flowers are unisexual, the plant is said to be *diclinous*; if both kinds of flowers are on one plant, it is *monœcious*, if on separate plants, *diœcious*. Other complications occur, and are mentioned below.] The more primitive existing flowering plants, however, the Gymnosperms and Chalazogams, are diclinous, and hence it is quite probable that this was the condition of the original ancestral forms.

Let us then picture to ourselves as a starting-point a plant with monœcious flowers, each consisting of an axis bearing numerous sporophylls, perhaps spirally arranged.

Fertilisation no longer occurs by means of swimming spermatozoids; these are functionally replaced by pollen-tubes, and there must be, before fertilisation can take place, a preliminary operation—*pollination*—consisting in the transport of the pollen-grains to the ovules. The earliest flowers must have depended upon the wind for this transport, and were therefore *anemophilous* or *wind-fertilised* (better *wind-pollinated*). It is evident that this mode of pollination is not economical; vast quantities of pollen must be produced to ensure that some shall reach the ovules. Comparatively few flowering plants (see below, p. 84) retain the anemophilous condition of their ancestry, and these have mostly acquired other characters which increase the chance of successful pollination. Besides the waste of pollen in transport, it is evident that there is much risk of damage to it from rain, for it is necessary to expose it so far at least as to ensure its being carried away by wind. Sporangia as a rule only open in dry air, and in this way the risk from rain is lessened. The close packing of the sporophylls upon the axis would also help to keep water from reaching the pollen.

A primitive type of *stamen* was probably something like a sporophyll of Selaginella, a small leaf with sessile pollen-sacs; this type survives in the Gymnosperms and perhaps in some Chalazogams, but in most flowering plants we find the familiar stalked stamen consisting of a *filament* bearing at the top an *anther*. The latter consists typically of two chief *lobes*, in each of which are two *pollen-sacs*. The filament is usually continued between the lobes by a sterile portion of tissue, the *connective*, containing a vascular bundle. This marks the back of the anther, the pollen-sacs forming the front. Down the middle, in front, is usually a groove dividing the lobes, and each lobe has another groove dividing its sacs. These latter grooves are termed the *lines of dehiscence*, for it is along them that the split usually forms by which the pollen escapes. [For exceptions, and other details of staminal morphology see below, p. 76.] This construction affords considerable advantages, even in wind-pollination, as compared with the simple sporophyll, but at the same time it probably increases the difficulty of protecting the pollen from rain. Since, however, this type of

stamen is almost universal, there is no room to doubt that the advantages overbalanced the disadvantages, even in the very beginning.

The primitive types of *carpel*, also, were probably sporophylls bearing one or more ovules. There can be no doubt that the ovule is morphologically equivalent to (*homologous* with) a megasporangium, though some of the details of the structure differ (*e.g.* we are not quite clear about the morphology of the nucellus and integuments). In practically all the Angiosperms (except some Butomaceae, Nymphaeaceae, &c.) the ovules are borne on the margins of the carpels, and upon the upper (ventral) side. Hence it is possible that the carpel of Cycas, as it now exists, may be a fair representation of the primitive carpel from which the carpels of the higher Angiosperms are derived. The Cycads, however, are probably derived from Pteridophytes by an independent route, and are not a branch of the main stem of Phanerogams at all; hence we must not hastily draw conclusions from them about the evolution of other flowering plants. It is possible therefore that in those Coniferae which have no ovuliferous scales we may find a nearer representation of this primitive carpel. For our present purpose, however, it is sufficient to imagine a leafy sporophyll bearing one or more ovules. The ovule has an *integument* enclosing a mass of tissue (*nucellus*) in which are several large cells (*embryo-sacs* or *megaspores*). The spores germinate in the ovules and form the female prothalli or gametophytes (*endosperm*) bearing archegonia. Fertilisation takes place when a pollen grain is placed on the apex of the nucellus; it developes its tube, as elsewhere described (p. 43 and article Gymnospermae), and this burrows down to the archegonia. The first step in the evolution of the carpel may be traced by a comparison of Gymnosperms and Angiosperms. The carpel probably became infolded upwards in such a way as to form a hollow receptacle, the *ovary*, containing the ovules, borne in rows on its ventral margins. The tip of the carpel, in the line of the midrib, now formed the *style*, ending in the *stigma*, the receptive portion to which the pollen grains must be applied to ensure fertilisation. At a very early period in the history of the Angiosperms, probably fertilisation was chalazogamic (p. 44 and

article Chalazogamae), as it still is in Casuarina, &c., but most of the Angiosperms seem to be porogamic. The number of embryo-sacs, too, soon became reduced to one ; few exceptions to this rule are known, except in those plants with chalazal fertilisation. The female prothallus or endosperm, too, was not formed till after fertilisation (see article Angiospermae). Such a typical carpel as we have described is well represented in many Ranunculaceae, *e.g.* hellebore or aconite.

What we have said above will be sufficient also to show the error of terming stamens and carpels modified leaves, as if they were derived from the leaves of the vegetative shoot. To solve the question of their origin and significance we must obviously go back to the Pteridophytes. We may indeed expect to find that most of the phenomena of the morphology of the reproductive shoot are paralleled in the vegetative, but we must beware of forcing comparisons too far, and assuming, as is so often done, that the one is derived from the other. If indeed there be any derivation, it is probably of the vegetative from the reproductive organs, not *vice versa.*

At an early period of time, perhaps about the same date as the separation of Gymnosperms from Angiosperms (if indeed this took place at all and they are not independently derived from separate stocks of Pteridophyta) the flower, if not already hermaphrodite, became so, and we may suppose that the upper sporophylls were female, the lower male, since this is the rule in existing seed-plants. Our flower may now be pictured as an elongated axis with stamens and carpels, the former showing filament and anther, the latter ovary and stigma. The various sporophylls are all quite free from one another (*polyandrous* and *apocarpous*), and there are no other leaves near to them upon the axis, *i.e.* the flower is *naked* or *achlamydeous.* The receptacle being convex and the carpels highest upon it, the rest of the flower is *hypogy-nous* (below the *gynœceum* or carpellary portion ; the stamens taken together forming the *andrœceum*). The flower too was anemophilous. No flower now existing quite represents this state of things. There are many naked flowers, but in studying them we are at once met with the question, " are they primitively naked (*i.e.* have all their ancestral forms,

however far they be traced, also been naked) or are they naked by reduction, *i.e.* by the loss of a perianth possessed at some period by their ancestry?" Those naked flowers which occur among the Chalazogams are probably primitively so, their other characters attesting their antiquity, and perhaps the Gramineae and some of the lower Dicotyledons may also be included here, but such flowers as Achlys, Euphorbia, Altingia, &c. are certainly naked by abortion, occurring as they do in families most of whose flowers are not naked.

We may now go on picturing the further upward evolution of the flower and the differentiation of its parts accompanying the differentiation of its functions. The upward progress has, as usual, followed many lines; sometimes a particular function is performed by one part of the flower, sometimes by another, and these parts are variously modified in structure to suit the various purposes they fulfil.

One of the earliest phenomena in the evolution seems to have been the formation of a *perianth* or envelope of non-reproductive leaves around the essential organs of the flower. The origin of the perianth is a subject beset with difficulty; there are various explanations possible. It may have been originally derived from true vegetative leaves which gradually grew closer and closer upon the shoot to the stamens and carpels, or it may have been derived from sporophylls (probably stamens) which gave up their spore-producing function, and in consequence of this probably became larger in size by the diversion of the food materials formerly given to the spores; or again, it is possible that both these views have some truth in them. However it may be, it is probable that the perianth first appeared as a few greenish or brownish coloured leaves at the base of the flower, and, by covering the stamens and carpels in the bud, performed for them the important function of protection from the weather. All the leaves of the perianth being alike, it may be termed *homochlamydeous*, and, the individual leaves being like the sepals of a higher type of flower in colour and texture, the perianth may also be termed *sepaloid*. True simple perianths of this type occur in some of the lower cohorts both of Monocotyledons and Dicotyledons. We have again to be on our guard however

against cases in which abortion of part of a double perianth has occurred, *i.e.* against true apetalous flowers (see below).

At an early period, too, the parts of the flower became arranged in whorls rather than in spirals, the tendency being apparently to the formation of one whorl of perianth, and two or three each of stamens and carpels. The flower is said to be *cyclic* when all its parts are in whorls, *acyclic* when all are spiral, *hemicyclic* when some are in one, some in the other, arrangement. In the orders of cohort Ranales may be found many cases of acyclic and hemicyclic flowers. With this formation of whorls is also bound up a condensation of the receptacle from the very elongated form to a simple convex structure. The members of the various whorls were at first probably equal in number, and those of each whorl alternated with those of the whorls next to it.

At about the same period, perhaps, the transition from wind-pollination to insect-pollination (*entomophily*) began, and from this period the evolution of flowers went on hand in hand with that of insects, and is best studied in connection therewith. It is not difficult to imagine how the transition began. Pollen is formed in great quantities in anemophilous flowers and is a very nutritious food. The earliest flying insects would only have very short lips, but finding the pollen freely exposed would be able to feed on it, and in this way might get into a regular habit of flower visiting. Pollen adhering to their bodies might thus be carried from flower to flower, and self-pollination also might be favoured by the insect carrying pollen from anther to stigma in the same flower. Whether the original insect-pollination was cross- or self-pollination, it would probably be more economical than wind-pollination, and therefore be retained as advantageous in the struggle for existence. If, as we have suggested, the primeval flowers were diclinous, cross-pollination was necessarily the earliest arrangement, and we may imagine that, when flowers became hermaphrodite, crossing was still provided for by the adoption of some of the mechanical arrangements described below, whilst the propinquity of stamens and carpels would enable self-pollination to be more easily resorted to at the last. If, on the other hand, flowers were primevally hermaphrodite, it would seem likely that they were usually self-

pollinated, though crossing would frequently occur as the pollen was blown about by the wind, especially if they were plants of social growth.

When insect-pollination began, the attraction of insects from a distance, and their remuneration on arrival, were probably both functions of the androeceum. Afterwards differentiation began, and other modes of attraction and remuneration appeared. The secretion of *honey*, by special organs termed *nectaries*, gave a great advantage to those flowers possessing it and soon became almost universal. Perfumes, too, aided in the attraction of insects from afar. From a morphological point of view, however, the most interesting feature was the formation of a second whorl of perianth-leaves, of bright colour, attracting insects by their conspicuousness. This new structure was the *corolla*, formed of *petals* free from one another and alternating with the stamens on one side and the leaves (*sepals*) of the primeval perianth (now termed the *calyx*) on the other. Such a perianth is termed *heterochlamydeous*, if the whorls differ in colour and texture.

The origin of the calyx is, as we have seen, a doubtful point; that of the corolla is almost equally so, but the balance of probability is in favour of the view that petals are modified stamens. Every step towards economy of pollen in the transition from anemophily to entomophily will naturally be accompanied by a reduction of the quantity produced. This may be effected in two ways, by reduction of the size of the anthers and by reduction of the number of stamens. Both of these probably occurred, as a comparison of existing flowers indicates. Now we know, from the phenomena of double flowers, &c., how readily stamens become *petaloid*, and it is easy, therefore, to imagine the outer stamens of a primitive flower becoming in this way transformed into a corolla. Many flowers in such orders as Ranunculaceae, Nymphaeaceae, &c. show phenomena supporting this view. [Most of the text-books quote such cases as the transition forms between petals and stamens in Nymphaea as proofs of the origin of stamens from petals; it is obvious that the argument is equally good if reversed, and it is also *à priori* far more probable in this form, as a moment's consideration of the intermediate forms will show.] If we

accept the view of the derivation of the corolla from the androeceum, we have a very pretty case of the differentiation of an organ into two, accompanying the differentiation of its function into two also. It is possible, too, that the original nectaries were also derived from stamens which as pollen-producers had become supernumerary; numerous cases of abortive stamens secreting honey occur in existing flowers.

The number of carpels was, as we have seen, probably considerable in the primitive flowers and, so long as pollination was uncertain, would very likely remain large, but, as the transport of pollen to the stigmas became more certain, a reduction in number of the carpels might take place, while the number of seeds ripened would remain as large as ever. Very few existing flowers have more than one whorl of carpels, and we may therefore picture this as being the case also in the primitive entomophilous flowers with which we are now dealing.

We have now brought the flower in its upward evolutionary progress to that condition which the older morphologists term 'typical'; it possesses all the important parts ever found in flowers, but they are in the simplest condition and all independent of each other. The nearest approach to such a flower in existing species is found in some Crassulaceae, Alismaceae, &c. The further differentiation beyond this point has followed many lines, the chief of which we shall endeavour to point out.

Comparatively few flowers of the present day retain the separate (*apocarpous*) carpels of the primitive gynoeceum; in most cases *cohesion* of the carpels, to form a *syncarpous* gynoeceum, is the rule. At first probably the union was only at the base, as may still be seen in Helleborus; then it gradually became more complete (various stages may be seen in species of Saxifraga) till only the styles were free, and finally in many cases these too became united into a simple style with free stigmas, or even into a single style and stigma, as seen in Primula. This evolution of the gynoeceum evidently tends to economy and certainty in pollination as compared with the apocarpous condition.

From this point onwards the differentiation and evolution of the flower and its parts is very closely bound up with that of insects, and we shall consider them together.

The *insects* which visit flowers belong to various groups, of which the most important are:

(1) *Hemiptera* (bugs &c.): no special adaptations to floral diet; few flower-visiting species.

(2) *Coleoptera* (beetles): many flower-visiting species. The beetles are as a rule only able to lick freely-exposed honey, their tongues being very short; a few have tongues 3 to 6 mm. long. The commonest flower-visiting genus in Britain is the small bronze-black Meligethes.

(3) *Diptera* (flies): very numerous flower-visiting species. The mouth-parts are often highly modified for feeding on honey and pollen. For our purpose we may divide the flies into long-tongued and short-tongued. The former include the Syrphidae (drone- or hover-flies) and a few others, the latter all the remaining forms. The former confine themselves to a floral diet and are clever in finding concealed honey; their tongues vary in length from 4 to 12 mm. Many flowers are specially adapted to, and visited by, them. The most common genera in Britain are Eristalis, Platychirus, Syrphus, Rhingia, &c. The short-tongued flies are much less highly adapted to floral diet; many feed also on carrion &c. (some flowers, *e.g.* Arum, Rafflesia, Stapelia, &c., have availed themselves of this habit by acquiring a carrion-like smell); their tongues are short (less than 4 mm.) and they are rarely skilful in finding concealed honey. The commonest flower-visiting genera in Britain are Lucilia (small blue-bottle), Anthomyia, Scatophaga (dung fly), &c.

(4) *Hymenoptera* (ants, sawflies, ichneumons, bees, wasps, &c.): mostly flower-visiting species. They are all short-tongued except the bees. These latter are by far the most important group of insects in relation to the evolution of flowers. They collect both pollen and honey; the former is usually carried in the brushes of hairs on the hind-legs, into which it is brushed by the hairs on the tarsi. We may divide bees, for biological purposes, into short- and long-tongued, according as the tongue is shorter or longer than 6 mm. To the former group belong such small bees as Halictus, Andrena, &c.; to the latter chiefly the hive-bee (Apis) and the humble-bee (Bombus). There are a very great number of plants with flowers adapted to pollination by bees, especially the long-tongued forms.

(5) *Lepidoptera* (butterflies and moths): all species flower-visiting. Their tongues are on the whole about as long as those of bees, but some species, mostly Sphingidae (hawk-moths), have them of extraordinary lengths, *e.g.* in Britain that of *Sphinx convolvuli* is 80 mm. long, whilst some forms even reach 300 mm.

For further details see Muller's *Fertilisation of Flowers* and entomological text-books.

One great direction followed in this evolution has been the formation of tubular structures in flowers, narrowing the entrance to the honey. The simple flower we have just been dealing with has its honey freely exposed, so that it may be licked by the shortest-tongued insects. Many flowers of this kind still exist, and form a biological class, "flowers

with freely exposed honey." It is termed for brevity class **A**, and contains such flowers as those of species of Saxifraga, Parnassia, Galium, most Umbelliferae, Hedera, &c. Observation shows that the insect visitors to flowers of this class are chiefly short-tongued; bees and Lepidoptera rarely visit them[1]. So long as all insects were short-tongued, this type of flower would perhaps succeed well enough, though it is exposed to the risk of having its honey spoiled by rain. The upward evolution of flower-visiting insects seems to have proceeded in the direction of longer-and-longer-tongued forms. The cleverness, too, of the insects, in finding concealed honey, or in dealing with hanging or irregular flowers, is largely correlated with the length of their tongues. A slight lengthening of tongue in a primitive insect would probably be advantageous to it even in dealing with flowers of class A, but it might be a disadvantage to the flower by preventing the insect from entering far enough to touch the stamens or stigma. Be this as it may, however, the concealment and protection of the honey, by the formation of a tubular structure in the flower, seems to have kept pace with the lengthening of the insects' tongues. The next stage is represented in existing flowers by those which form the class **AB**, "flowers with partially concealed honey." Such are Ranunculus, Sedum, Cruciferae, Fragaria, Potentilla, &c. The visitors to flowers of this type require tongues of 2 to 6 mm. or more in length. Observation shows that the actual visitors are those whose tongues are long enough to fit the flowers; those whose tongues are too short rarely visit the flowers. Bees and Lepidoptera visit flowers of this class more often than those of class A, but the bulk of the visitors are the short-tongued Hymenoptera, and the longer-tongued flies. From a morphological point of view the chief interest is to notice the ways in which concealment of

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[1] No student should omit to spend a few fine afternoons in observing the insect visitors to flowers of the various biological classes. Even if he is unable to recognize the insects he will be able to observe their length of tongue, size of body, &c., and compare these observations with those made on the depth of tube in the flower and so on. He should also notice the numbers of visitors of each kind that visit the flowers and compare the proportions with the class of flower; see below (p. 101). and refer to *Annals of Bot.*, June 1895, or to Müller's *Fertilisation of Flowers*, and other books.

the honey is effected. In Ranunculus, &c. it is merely by the position of the stamens, &c., a method which does not admit of much further elaboration. In Cruciferae the sepals stand stiffly erect, thus making the lower part of the flower a narrow tube, as is well seen in wallflower. In Fragaria, Potentilla, &c., we see the beginnings of *perigyny* of the flower. and this is a point of great importance. The earliest flowers had, we have seen reason to suppose, elongated axes ; we have followed the condensation of the axis to the simple convex form that it has in hypogynous flowers, and now we must imagine this condensation proceeding yet further in many flowers. The receptacle in its development becomes flattened on the top by the more rapid growth of the sides, so that as seen in section it has a kind of $\triangledown$ shape. This stage is still represented in many plants. In Acer, Ruta, and many other plants of the orders placed in Disciflorae by Bentham and Hooker (see Chapter II.) the flattening is above the calyx, so that a *disc* is formed in the base of the flower, bearing corolla, stamens and carpels. In Rosaceae, Crassulaceae, &c. (most of the Calyciflorae of Bentham and Hooker), however, the calyx also is borne on the edge of the flattened receptacle. Usually the growth of the sides goes on so far as to make the upper surface concave, so that a shallow or deep cup is formed, with the calyx spring-ing from its margin. The texture of the cup is usually similar to that of the calyx, often to such an extent that it is impossible to point out by mere inspection of the outside where one ends and the other begins. The older morpho-logists termed the cup the *calyx-tube*, imagining that the calyx was composed of united sepals (*gamosepalous*). The corolla usually springs from the margin of the cup, and the stamens lower down in it.

Following any of the evolutionary lines we have thus indicated, many flowers probably arrived at the further condition represented in the existing flowers of class **B**, with fully concealed honey. Such are Anemone § Pulsatilla, the Silenoideae (Caryophyllaceae) with shorter tubes (such as Gypsophila), Geranium, Epilobium, Rubus, Polemonium, Veronica, Mentha, Calluna, &c. Some of these, as exami-nation of them will show, attain their purpose by concealing the honey with the stamens, &c., others by aid of the calyx,

which shows a further advance in being gamosepalous. Others again are more deeply perigynous, the receptacle becoming more deeply hollowed and tubular, whilst in the four genera last mentioned we find exhibited the new and important phenomenon of a corolla with combined petals (*sym-* or *gamo-petalous*). The visitors to flowers of this type are the smaller bees, many Lepidoptera, and the long-tongued flies, with a few of the larger bees. If we compare the flowers of class B with those of class A, we see that the former have gained in the protection of the honey, pollen, carpels, &c., but at the expense of losing the visits of the shorter-tongued insects. This loss, however, is more than compensated for by the superior cleverness and activity of the longer-tongued visitors; the latter, too, are usually found to confine their visits during one flight to few or even to one species of flower, so that much less pollen is wasted by them than by the more stupid insects which visit flowers more indiscriminately. The advantage to an insect of keeping (as bees largely do) to one kind of flower as long as possible, is evident, for the insect will, so to speak, 'get its hand in' for the particular flower, and be able to visit far more flowers in a given time than if it frequently changed from one species to another.

A further lengthening of the tube of the flower, beyond the stage we have considered, will exclude the shorter-tongued insects and allow only bees and Lepidoptera to get the honey. The highest stage in this line of evolution is seen in many flowers of class **F** (Lepidoptera flowers). Silene (the longest-tubed forms, like *S. inflata, nutans* &c.), Lychnis, &c., have a gamosepalous calyx, Oenothera, Daphne sp., Cuphea, &c., a long tubular receptacle, some Gentians, Ericas, Primulas, &c., a long tubular gamopetalous corolla.

Let us now return once more to the flowers of class A and trace another line in which evolution seems to have proceeded. The genus Saxifraga may perhaps serve as an illustration. In it we see some species with almost hypogynous flowers; others have a more cup-like receptacle, but the carpels are united at the sides to the cup. .Some show this phenomenon to a very slight extent, others to such a degree that only the styles remain free, the ovary being completely immersed in the hollow receptacle. Such

an ovary is termed *inferior* (as contrasted with the *superior* ovary of hypogynous and perigynous flowers), and the other parts of the flower are *epigynous*. It seems probable enough that such a series of stages may have occurred in the original evolution of epigynous flowers; it is at any rate improbable that many were derived from perigynous flowers with any important depth of tube. The first epigynous flowers would probably belong to class A with honey freely exposed on the epigynous disc, as we still see it in Umbelliferae, ivy, &c. From this point we may picture to ourselves the whole upward progress above sketched taking place, and deeper and deeper tubes being evolved. We see representations of the process still before us in the orders Umbelliferae (polypetalous, honey freely exposed), Rubiaceae (gamopetalous, tube of corolla of all depths, from the 1 mm. of Galium to the 30 mm. of Ixora), Campanulaceae (flowers of class B) and Compositae. A few of the Campanulaceae, most Dipsaceae, and the Compositae have flowers with depth of tube &c. as in class B, but as they have aggregated inflorescences and are thus more attractive to insects, besides being on a higher level in other biological features, they are grouped together as a class **B′** (flowers with fully concealed honey, in aggregated inflorescences).   .

If what we have said be ultimately proved to be true, it will appear that sympetaly has arisen from polypetaly by two distinct lines of evolution, and therefore that the Sympetalae do not form a true simple group all derived from a common sympetalous ancestor, but rather form two groups each with a common ancestor among the primitive Polypetalae.

In the various flowers we have so far been picturing to ourselves the symmetry has been supposed perfect, that is to say that the number of members of each whorl is the same, and each member of any whorl is like every other member of the same whorl in size, shape, texture, &c. If such a flower be divided in any vertical plane, the one half will be a reflection of the other. The symmetry is radial (p. 38) or *actinomorphic*, and the flower is *regular*. The nearest approach to this state of things may be seen in the Ranunculaceae, Rosaceae (see diagrams in Pt. II.), Crassulaceae, Ericaceae, &c. It more frequently happens than not that the symmetry, perfect in the outer whorls, is disturbed

by the fact of the gynœceum possessing too few carpels, as in most Sympetalae. Such flowers, however, are generally termed actinomorphic also. But if one or more members be missing from any of the outer whorls, or if in any whorl all the members are not exactly alike, then the flower is *irregular*. If it can be divided symmetrically in any plane, it is *zygomorphic* (see floral diagrams of Papaveraceae, Labiatae, Scrophulariaceae, &c.); if it cannot be so divided it is *asymmetric*, as in Valerianaceae. A great many families, *e.g.* Ranunculaceae, contain both regular and irregular flowers, whilst others, *e.g.* Labiatae, contain only the latter. The change from regularity to irregularity is then one which has begun independently in many branches of the phanerogamic tree. Of the determining and active causes we know no more than in the other cases already dealt with, but we may easily see the advantages of the change. Irregular flowers usually stand more or less horizontally, whereas regular ones are most often, perhaps, erect. That gravity has had a good deal to do with the appearance of zygomorphism is clear from the fact that in such flowers as Epilobium, &c., where the zygomorphism merely consists in a general upward bending of parts, the phenomenon does not appear if the plant be rotated on a clinostat so as to eliminate the action of gravitation. [See Vöchting in *Prings. Jahrb.* XVII. 1886, and Robertson in *Bot. Gazette*, 1888.] A flower that stands horizontally will obviously protect its pollen better, at least in those stamens that are uppermost, than one that stands erect. Further, when the flower has become horizontal, the only convenient track for the entering insect is by the lower side. We can easily imagine the evolution of such a flower into a zygomorphic one. The lower stamens and the style might bend over to come under the upper side of the flower, and this might develope into a protective hood, whilst the lower half of the flower (usually only the corolla) might enlarge into a conspicuous lower lip, forming the landing-place for insects. Flowers of this kind are seen in most Labiatae and allied orders, Orchidaceae, &c. If the lower half of the corolla, on the other hand, assumed the protective duties, we should get such a case as seen in the Leguminosae. This fact, that the flower has now only one track to the honey instead of many, is probably one of the chief advan-

tages of zygomorphism, as it enables the anthers and stigmas to be kept in the one place only and thus favours economy of pollen, &c. Flowers of this class, together with a few others, mostly hanging flowers, are visited chiefly by long-tongued bees and form the class **H** (bee-flowers). Their length of tube is usually that of a bee's tongue.

The two-lipped condition, however, is not the only form of irregularity. Very often one petal differs from the rest in shape, *e.g.* the lower petal of Viola is drawn out into a spur in which the honey is protected from short-lipped insects. Similar phenomena occur in Delphinium, many Orchids (Angraecum is the most remarkable), and also in many Sympetalae, *e.g.* Centranthus, Linaria, &c. Again, mention may be made of the irregular outer flowers of the condensed inflorescences of many Cruciferae, Umbelliferae, Compositae, Dipsaceae, &c. The advantage here seems to lie chiefly in the gain of conspicuousness.

We have seen reason to suppose that the upward passage to entomophily was marked by a reduction in number of the essential organs. As evolution proceeded and fertilisation became more and more economical and certain, we may suppose this reduction to have gone on further still. The lower existing types of polypetalous flowers have many stamens and carpels, the higher have generally two whorls of the former and one of the latter, and this whorl, too, is usually reduced in number. A very common case is for the outer whorls to be of 5 members each, the carpellary whorl of 3 members or even fewer. In the sympetalous flowers all but the lowest have only one whorl of stamens, and usually only two carpels, or even one. Not merely do the carpels tend to be reduced in number in the higher forms, but the number of ovules also is usually reduced. The Compositae, for instance, show only one in each flower. Other things being equal, the flower with the fewest ovules is the highest type, in entomophilous flowers; in anemophilous flowers the number of ovules is usually small; perhaps it increased during the change to entomophily.

A phenomenon that seems to accompany upward progress in sympetalous flowers is the union of the stamens to the corolla (*epipetaly*). This is evidently a saving of material, both in the stalks of the stamens themselves, and in the fact

that it enables the base of the corolla-tube to become narrower and thus protect the honey better. The phenomenon occurs in the higher types of both series of Sympetalae, *e.g.* in Compositae and in Labiatae.

We have now outlined the chief changes that seem to mark the evolution of the various existing kinds of flowers. Only those features have been dealt with that have been of wide significance and which, when once formed, have been handed down to large numbers of descendants (these as we shall see are the characters of most importance for classification). Innumerable minor changes in the morphology of the flower have taken place in different groups of plants, and are of importance in considering the classification or morphology of these groups. These will be indicated in part in the next sections. It must be understood that of the various evolutions described more than one has frequently occurred at once. To sum up briefly the main phenomena of importance in the floral morphology as above considered, we have : reduction in number of essential organs, transition from wind- to insect-pollination and from simple to hollow carpels, the acquirement of hermaphroditism, the formation of a perianth, the condensation of the receptacle and formation of whorls, cohesion of carpels, sepals and petals, adhesion of stamens to corolla, development of perigyny, epigyny, irregularity, and so on.

Special Morphology of the Flower. In the sketch above given we have called attention to the more important features in the morphology of the flower, endeavouring at the same time to show their meaning in the light of the theory of evolution and in connection with the gradual differentiation and perfection of their functions. In this section we shall briefly treat of the morphology of the parts of the flower in order and without reference to functions.

The flower usually stands in the axil of a bract and it is found that as a rule the same side of each flower on any plant faces the bract. Hence we have a convenient mode of describing the sides of the flower ; that facing the bract is *anterior*, that facing away from it, *i.e.* towards the original stem, is *posterior*. In drawing a floral diagram (see below) we therefore put in at the top the original stem upon which

the flower is a branch, and at the bottom the bract, to mark the orientation. Upon the axis of the flower itself there are usually one or two bracteoles, as we have seen. In Dicotyledons there are usually two, placed right and left (see floral diagram of Caryophyllaceae), in Monocotyledons commonly one, placed posteriorly (this is sometimes due to a union of two leaves). The lower bracteole is frequently marked α in floral diagrams, the upper β. The parts of the flower usually follow certain definite rules in their orientation with regard to the bracts and bracteoles. Only the calyx need be considered, as the inner whorls have their arrangement determined by the outer. Whilst, as we have seen, the parts of the flower are usually condensed into whorls, the calyx most commonly develops in a spiral way, the sepals appearing in consecutive order rather than simultaneously. The general rule, to which however there are frequent exceptions, in the formation of new organs at the growing point, is that each organ develops in the widest space left between its immediate predecessors. The position of the bracteoles illustrates this. When there is one posterior bracteole the parts of the flower are usually three in each whorl and the odd (first) sepal is anterior, as *e.g.* in Zingiberaceae (*q.v.*). With two bracteoles and three sepals the first sepal lies nearly opposite the upper bracteole and the odd sepal is median (either anterior or posterior). With two bracteoles and five sepals the same is the case (see Caryophyllaceae and Leguminosae). The arrangement is the same if the sepals appear simultaneously. If only two sepals occur they are placed antero-posteriorly (*e.g.* Cruciferae). Much labour and ingenuity has been expended in trying to harmonise these phenomena with the theory of phyllotaxy, as must needs be done if the old view of the morphology of the flower be accepted; we have seen above the error of this conception and hence such labour is now useless. [For further details of this much discussed subject, refer to Sachs' *History of Botany*, Eichler's *Bluthendiagramme*, and Schumann's recent works, *Morphologische Studien*, I. 1892, and *Neue Untersuchungen üb. d. Blütenanschluss*, 1890.]

The general structure of the *receptacle* or torus has been considered above (pp. 55, 61, 66, 67). We have seen that it may be cylindrical, convex, discoid, flattened, cup-like, or

even hollowed out so as to completely enclose the gynœceum. According to the shape, &c. of the torus the flower is, as we have seen, termed hypo-, peri- or epi-gynous. Sometimes outgrowths (*effigurations*) of the receptacle are seen, *e.g.* in Passiflora, Capparidaceae, Orchidaceae, &c. Sometimes the receptacle elongates between the whorls of floral members, *e.g.* in Lychnis between calyx and corolla, in Passiflora and in many Capparidaceae between corolla and stamens, in Capparis between stamens and ovary. If the elongated portion bear the stamens it is termed an *androphore*, if only the ovary, a *gynophore*. Other receptacular outgrowths are seen in epigynous flowers, *e.g.* the wings on the inferior ovary of Begonia, the thorns (which sometimes bear flowers) on that of Tetragonia, the nectariferous disc of Umbelliferae, Compositae, &c., and so on.

The *development* of the flower cannot be treated in detail here. The receptacle at first is always convex and remains so in hypogynous flowers. In perigynous flowers it becomes concave by the more rapid growth of the sides, and this process is carried to its limit in epigynous flowers. The organs appear as a rule in acropetal succession (p. 22), though there are many exceptions. The members of whorls which show cohesion when mature always appear independently of one another at first, and are united by the growth of the whole subjacent tissue. Similar phenomena give rise to adhesion (*e.g.* epipetaly of stamens). [For details see Goebel's *Outlines of Classification*, or better his *Entwicklungsgeschichte d. Pflanzenorgane* in Schenk's *Handbuch der Bot.*, also the magnificent figures and descriptions in Payer's *Organogénie de la Fleur*.]

We have dealt with the *symmetry* of the flower on p. 68. It may be noted that in zygomorphic flowers the plane of symmetry is usually the antero-posterior plane. Transverse zygomorphism occurs in some Papaveraceae (*q.v.*), Haemodoraceae, Anigozanthos, &c., and diagonal in Solanaceae, &c. Reference may also be made to the peculiar phenomena seen in Exacum, Saintpaulia and Cassia (*q.v.*). Recently, Macloskie (*Amer. Naturalist* and *Science*, 1895) has tried to show that right- and left-handedness such as occurs in these flowers is common in plants generally, in vegetative organs as well as in flowers. Twisting of the stalk of the flower

sometimes alters the plane of the symmetry, as in Lobelia, Orchidaceae, Fumaria, Impatiens, &c. The terminal flower of an inflorescence has sometimes a different symmetry from the laterals, *e.g.* in Ruta, Acer, Adoxa, Acalypha, &c. (cf. also the peloria of Linaria). In Ariopsis, Cyclanthus, Morinda, Lonicera, &c. more or less union of different flowers occurs. Mention may also be made of the *polymorphism* of the flowers of some Orchids, *e.g.* Catasetum.

The number of members in each whorl of the flower is usually the same, except in the gynœceum; this in most cases has fewer members than the outer whorls (or is *oligomerous*). The most common number in each whorl in Monocotyledons is three (*trimerous* flower), in Dicotyledons five (*pentamerous*); two, four and other numbers also occur in both groups. Many flowers in the cohorts Ranales &c. (see Chapter II.) are spirally arranged (p. 61). When the number of members in a whorl is more than ten, it is commonly termed *indefinite* (represented by the symbol ∞), but the name may also be given to such cases as the apocarpous gynœcea of many Ranunculaceae, where, though the number of carpels is small, it is very variable in different flowers. When the number of members is the same in every whorl, the flower is *encyclic*; when it is not so, *heterocyclic*. The number of whorls is expressed by terms such as *pentacyclic*, &c. The members of each whorl usually alternate with those of the whorl next below (outside); when they do not do so they are usually opposite to them (*anteposed*), as in Primula, many Caryophyllaceae, &c., where the stamens are anteposed to the petals.

Abortion or *suppression* of individual members of a whorl is common, especially in the gynœceum and andrœceum. Oligomery of the gynœceum comes under this heading, also such cases as the absence of the posterior stamen in Labiatae, &c., of some of the petals in Aconitum, &c., and so on.

Multiplication of members (*i.e.* the presence of several where we expect from the general structure of the flower to find only one) is usually due to *branching* or *dédoublement*, and is especially common in stamens, *e.g.* in some Myrtaceae (Calothamnus, &c.), Papaveraceae (Fumaria, &c.), Ricinus, Polygonaceae, Malvaceae, Cruciferae, Capparidaceae,

Guttiferae, &c. It occurs in the carpels of Nolanaceae and many Malvaceae, &c.

Cohesion (union of members of the same whorl) and *adhesion* (union of members of one whorl to those of another) are, as we have seen, frequent phenomena; the former may occur in any whorl, the latter chiefly in the androeceum. The free parts of a coherent corolla or calyx are termed the *lobes, teeth* or *segments. Irregularity* has been dealt with on p. 69.

The flower when young is in the form of a *bud*, in which the various organs are closely packed. The way in which they fit together is always the same for the same flower and often for a whole family, so that the arrangement in bud (*aestivation*) is a character of considerable importance in classification. Only the perianth need be considered. If the leaves or segments do not even meet one another by their edges (examined near the base) the aestivation is *open* (see corolla of Cruciferae in Pt. II.); if they just meet at the edges, without any overlap, it is *valvate* (corolla of Compositae); if they overlap, it is *imbricate* (calyx of Leguminosae). Of the latter, special cases are *convolute* or *contorted* (each leaf overlapping with one edge, underlapping with the other, as in corolla of Malva, Gentiana, &c.), and *quincuncial* (two leaves with both margins overlapping, two with both underlapping, one with one over-, one under-lapping, as in calyx of Caryophyllaceae); the imbrication is *ascending* when each leaf overlaps the one posterior to it (calyx of Vicia, see Leguminosae), *descending* when each overlaps the one anterior to it (corolla of Vicia). If the leaf-margins are turned inwards they are *induplicate* (corolla of many Compositae), if outwards, *reduplicate*. If the leaves are rolled up inwards like watch-springs (cf. leaf of ferns) they are *circinate ; e.g.* the petals of Hamamelidaceae.

The *perianth* may show any of the various conditions we have considered above : it may be in one whorl or in two ; if both whorls are alike in colour and texture it is *homochlamydeous*, if unlike, *heterochlamydeous*. In the latter case one speaks of calyx and corolla, but in the former (*e.g.* in most Monocotyledons) usually of the perianth as a whole. According to texture and colour, &c. the perianth may be sepaloid or petaloid. If there is only one whorl of perianth

the flower is *monochlamydeous*, if none at all, *achlamydeous*. We have considered above (pp. 59, 60) the difficulty of deciding whether these conditions are primitive or not. The perianth may be hypogynous, perigynous, or epigynous. The individual leaves are sometimes termed the *tepals*. They may be free from one another (*polyphyllous*) or united (*gamophyllous*).

Similarly the *calyx* and *corolla* may be hypogynous, perigynous, or epigynous; poly- or gamo-sepalous (or -petalous); regular or irregular, &c. The sepals are commonly leafy and green in colour, but sometimes are more or less woody (some Myrtaceae, &c.), or brightly coloured (Clerodendron, some Ranunculaceae, &c.). In many epigynous flowers they are much reduced, *e.g.* in Umbelliferae and Rubiaceae. In Compositae they are frequently represented by hairs or bristles, and so on. In Malvaceae, some Rosaceae (*e.g.* Potentilla) and Lythraceae there is an *epicalyx* of apparent stipular nature (see also Dipsaceae). The petals are usually of some other colour than green, and of delicate texture. They may be narrowed at the base, as in wallflower, into a *claw*. To the general form of the sympetalous corolla various names are applied, *e.g. tubular*, *funnel-shaped*, *campanulate* (bell-shaped as in Canterbury bells), *rotate* (wheel-shaped with little or no tube, as in Veronica), *salver-shaped* (ditto, but with long tubular portion, as in primrose), *spurred* (as in Linaria), &c. To both calyx and corolla there are applied terms indicating the length of time they last. If they fall as the bud opens they are *caducous*, if just after fertilisation, *deciduous*, if they remain round the fruit, *persistent*.

The *andrœceum* or stamens may be hypo-, peri- or epigynous; free from one another (*polyandrous*) or united. If they are united into one bundle, the term *monadelphous* is applied (*e.g.* in many Leguminosae, Malvaceae, &c.), if into two or more (these cases are usually cases of branching; see above) the terms di-, tri-, adelphous, &c. Sometimes the union is so complete as to include the anthers, and a *synandrium* is formed, as in many Araceae, Cyclanthera, Phyllanthus sp., Cucurbitaceae, &c. When two are longer than the other two, as in Labiatae, they are *didynamous*, when there are four long ones, *tetradynamous* (Cruciferae). When the anthers

are united they are said to be *syngenesious* (Compositae, Balsaminaceae). The stamens may be *epipetalous* (p. 70), or *gynandrous* (Orchidaceae, *q.v.*). The anther may be joined to the filament by its whole length (*adnate*) or by its base (*innate*) or may be balanced on it, forming a T (*versatile*). It may be *introrse* or *extrorse* (opening towards the centre or circumference of the flower respectively) ; the opening may be *longitudinal* (by slits along the lateral grooves, see p. 57), *transverse, valvular* (Berberis, Lauraceae) or by *pores* (Ericaceae, &c.). In Phacelia, &c. the opening is longitudinal at first and then the anther turns inside out. The anther has typically two main *lobes* or *thecae*, each with two pollen-sacs. The thecae are curiously twisted in Columelliaceae, Cucurbitaceae, Acalypha, Cochliostema, &c. Viscum and other plants have very numerous pollen-sacs ; Gaura and other Onagraceae, some Mimoseae, &c., have septa dividing up the sacs. In Zygophyllum, Amaryllidaceae, Hydrophyllaceae, &c., the stamens have appendages on the filaments, in Melastomaceae, Ericaceae, &c., on the anthers. The pollen is usually in small grains; in anemophilous flowers these are smooth, dry, and powdery, in entomophilous flowers usually waxy, warty and coherent. In the Asclepiadaceae and Orchidaceae the grains are united into pollen masses or *pollinia*. In Ericaceae, &c., they are united in *tetrads* or groups of four (the product of one spore-mother-cell). Lastly, mention may be made of the fact that when some of the stamens are aborted, they need not necessarily disappear, but may remain as *staminodes*; these may be large and petaloid as in Scitamineae (Cannaceae, &c.), or small and insignificant as in the female flowers of many dioecious plants, or they may form nectaries as in Loasaceae, &c., or ' sham ' nectaries as in Parnassia.

The *gynœceum* may be *superior* or *inferior* (pp. 66 and 68) ; *apo-* or *syn-carpous* (*i.e.* carpels free or united). The old term *pistil* is now used to denote the individual carpels in apocarpous flowers, and the whole gynœceum in syncarpous flowers. The term *ovary*, strictly used, denotes the hollow ovule-containing part of the carpel or carpels, but is often used as synonymous with gynœceum. The style and stigma have been mentioned above (p. 58) ; the style usually crowns the ovary but is sometimes *lateral, basal,* or *gynobasic* (La-

biatae, &c.). In many Apocynaceae, Asclepiadaceae, Ochna, &c., the style is simple but the carpels are free from one another; this seems to be a 'reversion.' In Pavonia, Goethea, &c., there are more styles than carpels owing to abortion of some of the latter. The stigmas, when separate, are usually as many as the carpels, but in Euphorbiaceae, &c., they are commonly branched. They are usually over the midribs of the carpels, but in Papaver, &c., over the placentae. In Orchidaceae, Asclepiadaceae, Aristolochiaceae, Candolleaceae, the androeceum and gynoeceum are more or less united into a *column* or *gynostemium.*

Turning now to the *ovary* or cavity of the gynoeceum, it is usually single in the carpel of an apocarpous flower. In syncarpous flowers there may be one or more cavities or *loculi.* If we imagine the carpels of the whorl to meet and unite by their edges only, we get an ovary with one loculus (*unilocular*), as in Orchids (see floral diagram in Pt. II.); if we imagine each carpel folded inwards as in an apocarpous flower and then imagine them completely united, we get an ovary with as many loculi as carpels, as in Zingiberaceae (three carpels; see Pt. II.). We have seen (p. 58) that with few exceptions the ovules are borne on the margins of the carpels, ventrally, on more or less swollen portions, the *placentae.* The placentae in the syncarpous unilocular ovary will evidently be upon the walls (*parietal*); the placenta of one carpellary margin is united to that on the adjoining margin, so that the number of placentae indicates the number of carpels. In the multi-locular ovary above described, each carpel has its own loculus and placenta. The latter being all aggregated round a kind of central axis in the ovary, are termed *axile.* If we imagine in this ovary the radial divisions or *septa* to disappear we get what is called a *free-central* placenta, seen in Caryophyllaceae (*q.v.*), Primulaceae, &c. In many cases the number of ovules is reduced to one in each loculus or on each placenta, and then the placentae are commonly *basal* or *apical*—at the base or apex of the ovary ; see Compositae, Caryophyllaceae, Plumbaginaceae, Umbelliferae, &c.

The placentae are often much swollen and project into the ovary cavity; this is seen in the axile placentae of Solanaceae, &c., and is sometimes very much marked in

parietal placentae, which then project into the ovary so far as almost to chamber it into loculi. In these cases their inner ends are often double (T-shaped) as seen in section. Each margin of a carpel most commonly bears one row of ovules, so that at each placenta there are two rows (see floral diagrams in Part II.), but sometimes there are more, *e.g.* in Viola, Solanaceae, Orchidaceae, &c. In a number of flowers the simplicity of the ovarial morphology is interfered with by the formation of *false septa*—outgrowths of tissue which chamber up the ovary. Such may be seen in Linum, Cruciferae, Astragalus sp., Gaylussacia, &c. Mention may again be made of the divided carpels of Nolana, &c. (see p. 75). Peculiar ovarial structure is also seen in Punica, Mesembryanthemum, &c.

The *ovule* may be sessile or on a stalk (*funicle*); it may be *erect, ascending, horizontal,* or *pendulous,* according to the angle it makes with the horizon when standing upon the placenta. It consists of a mass of tissue, the nucellus, containing the embryo-sac, and enclosed in one or two integuments, which spring from the base (*chalaza*) of the ovule and leave a narrow opening (*micropyle*) at the apex for the entrance of the pollen-tube (see Phanerogamae, &c. in Pt. II.). If the stalk be in a line with the ovule and united to it only at the base, the ovule is *orthotropous,* as in Polygonaceae; if the stalk be united to the side of the ovule and the latter be reversed so that the micropyle comes near to the base of the stalk, whilst the chalaza is at the tip, the ovule is *anatropous* (the most common case); if the ovule be merely united to the stalk at the chalaza and be itself bent into a ∩ shape, it is *campylotropous,* as in Cruciferae, &c. In anatropous ovules the ridge along the side, formed by the stalk, is termed the *raphe ;* whether this is dorsal or ventral is sometimes a point of great importance in classification (see cohorts Sapindales, &c. in Chapter II.). An intermediate condition between the ortho- and ana-tropous patterns is called *amphitropous ;* the ovule and stalk are at right angles to one another, in a T-shape.

Much labour and discussion were formerly given to the attempt to decide the morphological nature of the ovule, *i.e.* whether it was to be regarded as a 'modified' stem or leaf (see *e.g.* Eichler's *Blüthendiagramme* I. p. 43 and II. p. xv.

or Asa Gray's *Structural Botany*, p. 282). A consideration of what we have said above about the relation between the vegetative and reproductive shoots and between Phanero-gams and Pteridophytes will be sufficient to show the uselessness of such attempts.

Floral Diagrams. A most useful method of expressing many of the important features in the morphology of the flower is to construct its floral diagram. This represents an imaginary section through the bud, taken (if such were possible) so as to pass through the ovary and anthers, and through the parts of the perianth where the æstivation is most clearly shown. With the exception of the hypogyny or epigyny, the diagram shows most of the characters that are usually necessary for identification of the natural order and hence is of much use in classification. A number of diagrams are given in Part II. and should be carefully compared with the flowers themselves.

The stem of origin, bract, and bracteoles (if any) are first put in, as explained on p. 72, and then the other parts in their exact relationships. When cohesion of parts occurs, they are joined by lines, as seen in the calyx of Silene (Caryophyllaceae, Pt. II.); sometimes this is omitted, *e.g.* in the corolla of the diagram of Compositae, but it is best at first to be strictly exact. The anthers are drawn in section, thus showing the lobes and the extrorse or introrse opening. The ovary and ovules are also drawn in section so as to show the placentation, &c. When the stigmas are over the placentae, as in Cruciferae, they may be marked as is there done, and in cases like Compositae or Gramineae, where the ovarial structure does not show their position, this should also be done. The æstivation (p. 75) of the parts must also be attended to. For detailed floral diagrams of many orders see Eichler's *Blüthendiagramme.*

Floral Formulae. A convenient mode of expressing the number of parts of the flower and some of the chief features in their arrangement is a floral formula. Many examples will be found in Part II. The calyx, corolla, androeceum and gynoeceum are represented by the symbols K, C, A, G, respectively (perianth by P). After the symbol follows the number of parts; if the number be enclosed in a bracket it means that the parts are united, if not, that

they are free. Thus, K (5) means "calyx of 5 sepals, gamo-sepalous," A 3 means "androeceum of 3 stamens, poly-androus." If there are two numbers with a + sign between them, two alternating whorls are signified, *e.g.* A 3 + 3 means that the androeceum is of two whorls of 3 stamens each. The ovary if inferior is represented by the symbol G̲, if superior by G̲.

Description of Flowers in technical language. There is no better training in the accurate use of terms than descriptive botany; the student should describe every flower he dissects, and also draw its floral diagram. At first it will be well to select those flowers whose diagrams are given in Pt. II. The descriptive terms used are mostly given above (individual terms may be found by reference to the index). The following descriptions of common flowers will serve to show the order in which the parts are described, and the general form of a description.

Ranunculus bulbosus (buttercup).

Flowers terminal, solitary, on long angular and furrowed peduncles, regular, hermaphrodite, hypogynous. Sepals 5, polysepalous, oval, coloured at the edge, reflexed, with shaggy hairs. Petals 5, polypetalous, roundish, concave, with wedge-shaped basal nectaries, bright yellow. Stamens ∞, polyandrous, spiral; filament yellow, slender; anther linear, adnate, extrorse. Carpels ∞, apocarpous, superior, collected into a nearly spherical head, greenish; stigmas sessile, recurved; ovules solitary, ascending, anatropous.

Taraxacum dens-leonis (dandelion).

Flower-heads on long scapes, involucrate; the outer leaves of the involucre linear, acute, recurved, in several rows; the inner erect, in one row. Common receptacle flat, naked. Flowers all ligulate, hermaphrodite, epigynous with pappose calyx. Corolla sympetalous, ligulate, with 5 teeth, bright yellow. Stamens 5, epipetalous, with yellow introrse synge-nesious anthers. Ovary inferior, compressed, unilocular; ovule 1, basal, erect, anatropous; style filiform, bifid at apex; stigmas upon the inner surfaces of the branches.

For further details see such books as Lindley's *Descriptive Botany.*

Special Natural History of the Flower. We have dealt with the broad general features of this subject above,

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and have now to consider some of the important details, such as the modes of pollination, the mechanisms by which it is effected, the protection of the flower, its colours, &c.

The general *agents*, external to the flower, effecting pollination are wind, animals, and water. The flower may effect its own (self-)pollination without assistance from any of them, but is dependent upon their help for cross-pollination. Of existing flowers a small number are only cross-pollinated (if pollinated at all), having by mechanical or physiological means lost all power of self-pollination (*autogamy*). Others again, a somewhat more numerous group, are solely self-pollinated, having no arrangements for utilising in their service either wind or insects. The majority of flowers, however, occupy an intermediate position between these two extremes. They have arrangements, more or less perfect, for obtaining cross-pollination by external agents, while at the same time they are not so constructed as to be unable to perform self-pollination.

There is good reason, as we have partly seen, for believing the primeval angiospermous flowers to have been cross-pollinated. If they were, as is likely, diclinous, this must have been the case, and even in a hermaphrodite flower with a very elongated receptacle self-pollination would hardly be possible, the stamens being so much below the carpels. That there are many purely self-pollinated flowers now existing is undeniable, but it is much more easy to explain their features on the supposition of their descent from cross-pollinated ancestry than to suppose them primitively autogamous. This view is supported also by the fact that most of the striking examples occur in families or even in genera most of whose members are cross-pollinated. We have seen (p. 46) that there is a price to be paid for cross-pollination, and if the gain from the process should by any means become less than the cost, the plant will probably, if able to do so, revert to self-pollination. It is easy to imagine cases in which this might occur. Suppose an insect-pollinated species, A, in a certain district and suppose a new and attractive flower to arrive from another district and establish itself; this will draw off some of the visitors of A and perhaps upset the balance of gain and loss, causing the latter to exceed the former. We shall

then expect to find A tending in the direction of increased autogamy ; the result will probably be the gradual reduction of those characters by which its visitors were attracted, and it may gradually almost entirely lose them.

Suppose, however, that the introduction of the new species merely reduced A's profit but did not destroy it, then we might imagine A increasing its expenditure, so to speak, upon attractive characters, so as if possible to regain its former predominance. This will usually only be possible in plants which have stores of reserve-materials to draw upon, *capitalists*, as they have been termed, in contrast to annuals, &c. which have no reserves (*proletarians*). Of course, the balance between gain and loss may be affected in many ways. owing to the exceedingly delicate adjustment of the inter-relationships of the life of plants and animals in any district. The famous example of the effect of cats upon clover (Darwin's *Origin of Species*, p. 57) illustrates this. The introduction of cultivation and therefore of new forms of plants into a district may produce serious effects upon the general balance of life there, even in the parts of the district most removed from the cultivated area; *e.g.* a field of clover may draw off most of the bees from the wild flowers. In this connection it is of great interest to study the floral mechanisms and insect visitors of the different species of such genera as Epilobium, Phacelia, Geranium, Gentiana (see Pt. II. and Müller's *Fertilisation of Flowers*) or such families as Caryophyllaceae, where within a small circle of related forms every stage may be seen, from high types with complex mechanisms and cross-pollination down to low types with simple mechanisms and self-pollination ; or we may study the same species in different countries, finding very often a remarkable amount of difference in its mechanism, visitors and other characters. We may further call attention to the fact that purely self-fertilised flowers occur chiefly or only among entomophilous and not among anemophilous families ; the reason is not far to seek, for there can be comparatively little competition among wind-pollinated flowers for the services of the pollinating agent.

Let us then imagine the primeval flowers as cross-fertilised. We have seen that they must have been anemophilous (p. 57). Many anemophilous flowers exist at the

present day, and, as usual, in considering them we are met with the difficulty of deciding whether they are primitively so (p. 59) or have become so by degeneration from ento-mophilous forms.   When in a family whose members are mostly insect-pollinated we meet with one or two anemo-philous forms we are safe in calling these degenerate; such cases are Artemisia in Compositae, Pringlea in Cruciferae, Poterium in Rosaceae, and probably Thalictrum in Ranun-culaceae (see Pt. II. for details); intermediate cases of more doubtful nature are seen in Plantaginaceae, Poly-gonaceae (Rheum and Rumex), Salicaceae, &c.   With the exception of the Gymnosperms and the catkinate families (Betulaceae, Fagaceae, Juglandaceae, &c.), which we know from other evidence to be of a very ancient type, we cannot say with any certainty that any anemophilous flower now existing is really primitively so.   Hence we can only point out the general characters of anemophilous flowers without being sure in every case whether they are true anemophilous characters, evolved entirely in anemophilous plants, or are secondary, derived from characters of an entomophilous ancestry.   The first great necessity is an abundance of pollen, to compensate for the enormous waste in transport. This, in the primitive flowers, and in the existing Gymno-sperms and catkinate orders, is effected by the presence of a great number of stamens; in such forms as Gramineae, Cyperaceae, Potamogeton, Empetrum, Littorella, Urtica-ceae, &c. there are few stamens, but they have very large anthers; in Ricinus the stamens are branched (this is dis-tinctly a recently acquired character, for it is not found in others of the order).   The stamens all ripen at the same time, instead of successively as in entomophilous flowers (see Thalictrum).   The pollen is dry and incoherent (p. 77) so as to blow about easily.   It must be as far as possible pro-tected from rain; in most cases this is partly effected by the fact that the anthers only open in dry air; in the catkins the bract forms a pent-house over the stamens, in Urticaceae the stamens are folded inwards until the moment of dehis-cence, in Gramineae they are protected by the glumes and only emerge from them in dry air, and so on.   The pollen must be freely accessible to the wind; in the catkin orders, Platanus, &c. the pendulous inflorescence is easily moved

by wind, and the pollen, which often collects on the upper surfaces of the bracts, is shaken out. In the flowers with few stamens, the filaments are usually long, projecting beyond the perianth, &c., the anthers usually versatile, so that the stamens are easily shaken. In Grasses, &c. they are pendulous. The flower itself is pendulous in Rumex. In Urticaceae the pollen is expelled from the anthers by an explosion. Turning now to the gynœceum, it is evidently advantageous for the stigmas to be large and freely exposed so as to have the best chance of catching the floating pollen grains. Most anemophilous flowers have large bush-like stigmas, much larger and rougher than those of entomophilous flowers. The most remarkable is perhaps the stigma of Zea. Many anemophilous plants flower before the leaves appear, *e.g.* the catkin families; others, *e.g.* Grasses, &c., have the inflorescence well above the vegetative shoot, and are often of social habit. Both these facts are of great importance to economical pollination. An important point to notice is that the number of ovules in an anemophilous flower is generally very small; often only one is found. This may be correlated with the fact that there is very little chance of sufficient pollen reaching the stigma to fertilise many ovules, whereas in entomophilous flowers the pollen clings together in masses. The most notable exceptions to the rule are Juncus and Populus; the former is often self-fertilised, and this may be the explanation, but Populus cannot be thus explained.

It may be noted in conclusion that dichogamy (*v.* below) is common in anemophilous flowers, and, for some unknown reason, it is nearly always protogynous. For further details of anemophily see the orders and genera mentioned, also Sparganium, Triglochin, Ulmaceae, Elaeagnaceae, &c.

We have already traced in imagination the transition to insect-pollination; let us now consider it from another point of view. It is evident, that if a visiting insect is to be of any use, that part of its body which touches the pollen must also be the part to touch the stigma. In a diclinous plant this is easily enough managed, but when the flower became hermaphrodite, difficulties would arise. So long as insects merely sprawled about the flowers, feeding on pollen, it would

not, perhaps, be much disadvantage to have the stigmas at a distance from the anthers, as insects would probably touch them sooner or later; there would however probably be at least as much self- as cross-pollination, even with insect visits. When nectaries and perianth were more fully evolved, the track taken by the insect visitors would be more definite ; the same species of insect would visit the same species of flower always in the same manner. It would now become a necessity to place anthers and stigmas so as to touch the same part of the insect, *i.e.* they must generally be close together, and now would come in the difficulty of avoiding pure autogamy. The ways in which this is effected present a bewildering variety, but all have the same general underlying principle, to ensure cross-pollination as far as may be done without seriously affecting the certainty of setting seed. Some plants can risk more for cross-pollination than others; *e.g.* an annual plant must set seed well, and so we find most annuals fully capable of autogamy. Long-lived perennials on the other hand can afford to try mainly for cross-pollination, and may even become incapable of autogamy altogether. The factors which have produced the particular phenomena seen in the pollination of any given flower are very numerous and the problem to be solved before we can fully explain the phenomena is of a most complex description. Account has to be taken of vegetative reproduction, amount of storage of material carried on by the plant, climate, competition with other plants and so on. We find, on comparing the floral phenomena of the same plant in different countries, a remarkable amount of variation, and this is no doubt largely correlated with the variation in the general conditions of life, &c.

The most certain mode of avoiding autogamy, while keeping anthers and stigmas in positions to touch the same portion of an insect-visitor, is of course to have diclinous flowers. These occur in a number of Phanerogams, but in all but the Gymnosperms, the catkinate families, and perhaps a few others, the diclinous flowers are undoubtedly derived from hermaphrodite ancestors, as is clearly indicated by the male flower usually possessing rudimentary carpels, and the female rudimentary stamens. Examples may be seen in Sagittaria, Rhamnus, Begonia, Aucuba, Bryonia, Peta-

sites, Tussilago, and many others (see characters of orders in Pt. II.). Dioecism has the serious disadvantage of re-quiring a lot of male plants whose sole function is to produce pollen ; the chance of pollination, too, is less than in monœcism, and here again less than in cases of her-maphroditism.

The avoidance of autogamy in diclinism depends on the separation of the pollen and stigma in *space.* A widespread, almost universal phenomenon in hermaphrodite flowers is *dichogamy* or separation in *time*, by which is meant that the pollen is ripe before the stigma, or the reverse. The former case is termed *protandry*, the latter *protogyny*. If the dicho-gamy be complete, *i.e.* if the first stage be over before the second begins, the result will be the complete prevention of self-pollination, while at the same time the anthers and stigmas may occupy positions as close as possible to one another, or even, by aid of movement, occupy the same position, at different times. Completely dichogamous flowers are rare, and are usually such as are so attractive to insects as to ensure being sufficiently visited for cross-pollination, *e.g.* Aeschynanthus, Canna, Clerodendron sp., and some wind-pollinated flowers, *e.g.* Parietaria. Nearly all flowers are more or less dichogamous, but there is generally a considerable period of overlap of the male and female stages, during which self-pollination is frequently possible. This is more or less guarded against by numerous mechanical arrangements, to be dealt with below. Dicho-gamy is a variable phenomenon, the same species showing different degrees of it in different localities, and even in the same locality at different periods of the year. Protandry is most common in insect-visited flowers (good examples of simple protandry are found in Umbelliferae and Caryo-phyllaceae), protogyny in wind-pollinated flowers; the latter also occurs in a considerable number of entomophilous forms, *e.g.* many Araceae, Paris, Colchicum, Asarum, Chi-monanthus, Amorpha, Goethea, Aesculus, &c. A flower in which stamens and stigmas ripen together is termed *homo-gamous*, but hardly any case of true homogamy is known ; usually there is some difference in the time of ripening of the stamens and stigmas.

Another method of preventing autogamy is *self-sterility*,

i.e. incapability of a flower to be fertilised by its own pollen, even if pollinated with it. This is a condition which is very little understood; the same flower varies in this respect in different countries. Corydalis sp., Abutilon sp., Passiflora sp., and others may serve as examples. It is very improbable that this character has been acquired as a preventive of autogamy; it is probably a secondary result of other factors in the life of the species. A phenomenon of the same kind is *pollen-prepotency*. If a stigma on a plant A be pollinated from the stamens of A and from those of another plant of the same species, B, in many cases the ovules will be fertilised by the tubes of B, not of A, even if A has had a considerable start (provided of course that the tubes of A have not reached the ovules). It is obvious that if general, this is a fact of very great importance. No definite statement can at present be made, but experiments carried on of late seem to point to this result (see *Brit. Ass. Report*, 1895).

Allied to these is the remarkable phenomenon of *heterostylism*, first elucidated by Darwin (*Forms of Flowers*). It is seen in a typical condition in the primrose or cowslip (Primula) and in Lythrum (q.v.). In the former two kinds of flowers are found (*dimorphism*), in the latter three (*trimorphism*), each on a separate plant; they are distinguished by the different lengths of the stamens and styles. One flower of Primula for example has a long style and short stamens, the other a short style and long stamens; the length of the long organs is the same in the two flowers, and also of the short, as the diagram shows (A = anthers, S = stigma, B = base of flower). Darwin showed that complete fertility is only obtained (*i.e.* a full yield of fertile seed) when pollen is taken from long stamen to long style or from short to short, which of course involves cross-fertilisation. It is

$$\begin{array}{cc} A_1 & S_1 \\ S_2 & A_2 \\ B & B \\ \text{short-} & \text{long-} \\ \text{styled} & \text{styled} \end{array}$$

evident that this *legitimate* pollination will tend to be regularly effected by the visiting insects, which behave always in the same way upon the flowers. *Illegitimate* pollination (short and long) results in few seeds and these are more or less sterile. This is a remarkable fact for it is exactly the phenomenon seen in hybridisation, *i.e.* in crossing of two distinct species, and it thus breaks down the old method

of determining the specific value of two forms, by crossing them to see whether the offspring showed the infertility characteristic of hybrids. For further details of this subject see Lythrum in Pt. II., also Darwin *loc. cit.* Other hetero-styled flowers are found in the genera Pontederia, Fago-pyrum, Linum, Erythroxylon, Oxalis, Statice, Hottonia, Menyanthes, Pulmonaria, Faramea, Bouvardia, Mitchella, and many others. In Nolana, &c. the length of the stamens and styles is very variable and it is possible that experiment may show that there is here an indication of the peculiar sex-characters of true heterostyled flowers.

Another phenomenon of similar nature to those we have just considered is the peculiar 'distribution of sexes' met with in many plants. In many Labiatae, *e.g.* Thymus, Nepeta, some plants bear hermaphrodite flowers, others female flowers with aborted stamens and smaller corollas. This is termed *gynodiœcism* and is common also in Caryo-phyllaceae (§ Alsineae), Scabiosa, Plantago, and other plants. In these cases closer study usually shows the pre-sence of female flowers on the hermaphrodite plants also; sometimes all the plants are of this mixed type, and the species is then *gynomonœcious.* Under the latter heading come also such cases as those Compositae whose ray-florets are female. The corresponding cases of *andromonœcism* and *androdiœcism* are rarely met with; Veratrum is an example of the former, Dryas of the latter. Lastly, under the term *polygamy* are included such cases as those of Fraxinus, Rhus, &c., where male, female, and hermaphrodite flowers all occur, sometimes all on one plant, sometimes on separate stocks. This case leads on naturally to true mon-and di-œcism. We are very much in the dark as to the meaning of these phenomena. They cannot be regarded as adaptations (see Chapter III.) for ensuring cross-pollination, for they are not always inherited and vary much with country, climate, season, &c., to say nothing of the fact that they have not been proved to be of any advantage to the plants possessing them. Androdiœcism is almost cer-tainly a mere 'nutrition' phenomenon, the starved plants being male. In Veratrum the male flowers are at the top of the inflorescence and may very likely get less nourishment. Burkill has shown (*Linn. Soc. Journ.* XXXI., 1895) that in

several flowers with variable numbers of stamens and carpels
the number of these organs in any flower depends partly
upon its position in the inflorescence, and partly upon the
season of the year (it decreases as the season advances).
Here we have, perhaps, a gleam of light as to one of the
physiological methods by which that reduction of stamens
and carpels was brought about, which we have seen to be
so important a feature in the upward evolution of flowers.
Gynodioecism and gynomonoecism are probably also largely
nutrition phenomena, and in the few cases where they
appear with some constancy are perhaps on the way to
becoming hereditarily fixed, but of course no dogmatic
statement can at present be made (see *Proc. Camb. Phil.
Soc.* 1892–3, three papers).

Passing on now to the more purely mechanical arrange-
ments for regulating pollination, we find in the Orchids
(q. v.) one which in nearly all cases renders the flowers
incapable of pollinating themselves, though autogamy
might occur if an insect visited the same flower twice.
These plants are perennials with much vegetative reproduc-
tion ; this obviates the risk they would otherwise run of
extinction in bad seasons; they also set a stupendous number
of seeds in every pollinated ovary.   It is most instructive
to compare this order with the Compositae (see Pt. II.).

A somewhat similar state of things is found in the
Asclepiadaceae, but these flowers are more visited by insects
and do not set so many seeds.   There are also other
flowers in which self-pollination is fully prevented, but such
cases are rare, and autogamy may occur if an insect visit
the same flower twice.   Such are Mimulus, Martynia, &c.
(sensitive stigmas), Iris, Viola sp. (the open flowers), &c.,
and the fully dichogamous flowers above mentioned.   We
shall go on now to deal with a few of the more common
types of floral mechanism in which both cross- and self-
pollination occur, beginning with those best adapted to the
former.

The most simple and successful mode of ensuring the
best chance of a cross for the longest time, with the cer-
tainty (in most cases) of autogamy if the cross fails, is the
piston-mechanism found in Compositae and some Campanu-
laceae, where the style acts as pollen-presenter with closed

stigmas, and afterwards the latter open out. An instructive series of flowers is found in Campanulaceae, leading up to the perfected mechanism of Compositae (see Pt. II.). A second type of the piston-mechanism is that seen in Leguminosae (q. v.). Here autogamy is prevented in many cases by the fact of the stigma only becoming receptive when rubbed, so that no fertilisation can take place till the flower has been visited by an insect. We may also mention here the lever-mechanisms of Salvia and Roscoea, the pollen-cup of Goodeniaceae, &c. The mechanism of Leguminosae is curiously repeated in Collinsia, Schizanthus, Phlomis, &c. The style also acts as pollen-presenter in many Proteaceae. Many of the Compositae (Cynareae) have the mechanism varied in detail by a sort of explosive arrangement, and this is even more marked in many Leguminosae, *e.g.* Genista. Similar phenomena are seen in some Orchids, *e.g.* Pterostylis, in Caladenia sp., Candollea, Kalmia, Posoqueria, &c. This leads on naturally to the mention of such other cases of sensitive and motile organs in flowers as the stamens of Berberis, Sparmannia, Portulaca, &c. (see also above, Mimulus, &c.).

A very common arrangement is for the style to project a little beyond the anthers, so as to be touched first by the insect-visitor. The flower in these cases is usually nearly homogamous. Of course autogamy is nearly certain to occur in such flowers, but as it will not usually occur before the cross-pollination it is likely that prepotency of the latter is the rule. Such flowers are Lamium and many other Labiatae and allied orders, many Cruciferae, Ranunculaceae, &c., and many of the 'loose-pollen' flowers mentioned below. In flowers of this kind every gradation is found from those in which cross-pollination is the rule to those in which it rarely occurs.

Another interesting mechanism is found in the Rhinanthus group of Scrophulariaceae (Euphrasia, Bartsia, &c.), Acanthus, &c. It may be termed the *loose-pollen mechanism.* The pollen, contrary to the usual habit in entomophilous flowers, is dry and powdery as in wind-pollinated forms. It is held loosely in a box formed by the stamens under the upper lip of the flower, and the parts are so arranged that the entering insect shall open the box and receive a shower

of pollen upon its head. Some of these forms are dichoga-
mous (protandrous), others merely have the stigma pro-
jecting beyond the 'stamens. Transition forms occur in
Euphrasia, &c. A second type of this mechanism is found
in the hanging flowers of Borago, Solanum sp., Erica, Cal-
luna, Cyclamen, Soldanella, Galanthus, &c.

Simple dichogamy with movement of the essential organs
so as to place first one and then the other in the track of an
entering insect, is very common. We have quoted some
extreme cases above. Others, in which there is more or
less possibility of autogamy, may be seen in Scabiosa,
Lonicera, Scrophularia, Teucrium, Umbelliferae, Caryophyl-
laceae, Delphinium, Aconitum, Geranium, Ruta, Epilobium,
Malva, and hundreds more.

Another interesting group is the *trap-flowers*, where by
some arrangement the visitors are entrapped and are either
suffered to depart at once by another road past the essential
organs, or are held prisoners till the later stage of the flower
(*i.e.* they are captured in the female stage of the dichogamy
and held until the pollen is shed). To the first class belong
Cypripedium, Coryanthes, Stanhopea, and other orchids, &c.,
to the second Arum and other Araceae, Aristolochia[1], Cero-
pegia, Aspidistra, Magnolia and others.

So far we have dealt with mechanisms in regard to the
favouring of cross-pollination. We have now to deal with
arrangements for autogamy, which are equally common,
even in most of the highest types of flowers. Thus in Com-
positae the final curling up of the stigmas, in a very great
number of flowers the withering of the corolla, in others
merely the movements of insects in visiting, bring pollen
and stigma into contact with one another. Details will be
found in Pt. II. under the various mechanisms treated.

The most interesting mechanism of this class is the pro-
duction, seen in a number of plants, of a second type of
flower which does not open and in which therefore only
self-pollination can occur. Such *cleistogamic* flowers are well
seen in Viola (q.v.), Oxalis, *Lamium amplexicaule, Salvia
verbenaca,* and many others ; they are frequent in Legumi-

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[1] Note that here a tube occurs in the flower, without any apparent
reference to insects' tongues (p. 64).

nosae. A consideration of all cases of cleistogamy shows that these flowers are usually produced either on shaded parts of the plants, or in the colder and darker seasons of the year. Vöchting (Einfl. d. Lichts, &c., in *Prings. Jahrb.* 1893) has shown that in plants that normally produce both open and cleistogamic flowers a reduction of the amount of light results in the production of the latter kind only. Other observers have shown that probably temperature and other conditions (those in general which reduce nutrition) are determining factors also (see *Linn. Soc. Journ.* xxx. 1893, p. 295, and *Science Progress*, Nov. 1895). Though these are determining factors, and their effect in any plant is to check the formation of open flowers, cleistogamy is not a phenomenon to be put on the same level with gynodiœcism, for it is hereditary, as well as advantageous to the plant possessing it, and cannot be artificially produced in plants not showing a tendency towards it. We may note that in chickweed (*Stellaria media*) the winter flowers tend to cleistogamy, and in water-plants the flowers when submerged are often pollinated in the bud. Lastly, in Myrmecodia, &c. only cleistogamic flowers are produced. These show by various characters that they have been derived, comparatively recently, from open flowers, and may be compared with the reduced autogamous flowers of such plants as *Senecio vulgaris*, &c.

Many of the regularly self-pollinating flowers, such as *Senecio vulgaris*, Capsella, &c., have a very wide distribution. This is explained by Wallace by the supposition that small changes of climate, &c., react upon the organism in the same way as cross-fertilisation, increasing its fertility, strength of constitution, variability and so on. The wide distribution of many cross-pollinated flowers is prevented by the circumstances of insect distribution. Many wind-pollinated flowers, however, are widely distributed.

The subject of the *colours* of flowers—and indeed of colour in plants generally—is one of considerable difficulty, and we shall only attempt a brief sketch of some of the outstanding facts, &c. The green colour of the vegetative organs is due to the presence of chlorophyll in certain specialised parts of the cell-protoplasm, known as *chloroplastids*. Green is rarely seen in the corolla of flowers,

though there are several interesting cases, *e.g.* Deherainea. The colours most often seen are yellowish-green, yellow, red, white, blue and shades of these or intermediate colours; yellow and white are the most common, blue the least so. If we investigate the source of the colour microscopically, we find that yellow flowers nearly always possess *chromoplastids*, protoplasmic bodies containing the yellow colouring matter. Some red flowers, and a very few blue ones have chromoplastids also. Most red flowers and nearly all blue, purple and violet ones have the colouring matter dissolved in the cell-sap. White flowers have colourless sap and plastids. This difference explains the fact that in the variations of colour so often seen, it is exceedingly rare for a green or yellow to pass to blue, or the reverse. All flowers, whatever their colour, seem to vary most easily towards white, and this is easily understood after what has been said above. This subject of colour-variation shows many points of interest. In the same individual flower, most Boraginaceae vary from red to blue as the age of the flower increases; the spots in Aesculus vary from yellow to red, the corolla of Myosotis sp. from white or yellow to blue, and so on (see Ribes, Fumaria, Diervilla, Arnebia, Cobaea, &c.). In some cases the flowers of a given plant differ in colour in different years. Turning now to the case of a whole species, there are many which show different colours in different flowers; sometimes these are special varieties or races, sometimes, as in Polygala, merely individuals otherwise exactly alike. The most striking varieties in colour may be seen in the cultivated forms, but they follow the same rules as the wild. In both cases it is found that for each species there is a certain range of colour beyond which it cannot be made to go in cultivation, and does not go in nature. By hybridisation and in other ways mixtures of colours may be produced, and every variety of shade and sometimes of variegation, but beyond certain limits the species cannot be made to pass. These limits are found on examination to be as a rule the colours found in the genus to which the species belongs. As an example, take the genus Dianthus. Some species show red, some white, some yellowish or purple-violet corollas, but none blue. Now in the cultivated pinks and carnations (*D.*

Caryophyllus) red, white, yellowish, and violet colours are known in every shade, mixture and variegation, but no efforts of horticulturists can produce a blue carnation. Other examples are found in the stock (Matthiola), wall-flower (Cheiranthus), aster (Callistephus) and most other cultivated flowers. Sometimes the range of colour in the species is that defined by the order rather than by the genus. A great many flowers do not normally vary in colour at all, and horticulturists sometimes find considerable difficulty in starting the variation necessary before new races can be obtained. The most common method is change of soil, manure, light, heat, &c. All these conditions have in nature certain influences on the colour of flowers (no definite rules can be framed, as two flowers of the same colour but of different species are often affected in opposite ways by the same agent), and when all are changed together, the plant seems as if it received some kind of a shock which may cause variation. Once variation in a hitherto fixed colour can be started it often continues for a long time, keeping, however, within certain limits, as we have explained. It is to be noted that with the exception of the long cultivated hyacinth, blue flowers do not vary to yellow, even if there be yellow species in the genus. Red varies towards yellow rather than towards blue. All colours vary readily to white.

Turning now to the question of the meaning and function of colour in flowers there can be no doubt that it is largely bound up with pollination by insects. If however we set out only from the higher plants, we shall as usual go wrong, and come across cases that cannot be explained in the light of the information there obtained. The spores of Cryptogams are generally coloured, and the most usual colour is yellow or brown, less often a red or green. What the meaning of this fact is, we do not know. Colours are well-known to appear in many chemical reactions and it is quite likely that many of the colours of plants and animals are of this accidental kind without any particular significance in the life-history. Or it may be that the colour of spores protects them from the action of light (which is very fatal, for example, to the spores of bacteria). However this may be, yellow is prevalent in spores proper and in their repre-

sentatives the pollen grains, and the conspicuous colour of many anemophilous flowers, *e.g.* Abies and other Conifers, Corylus, &c., some Grasses, and so on, is no longer a surprising exception, as it is if colours are regarded as only concerned with insect-visits. If now the corolla was derived (p. 62) from stamens, it would seem likely that its colour was yellow at first and that all the other colours are subsequent derivatives. Of these, red and blue are probably the highest types, and are found chiefly in flowers of high organisation.

In dealing with the question of the colour-sensitiveness of the eyes of insects we must remember the limitations of our own. There is good reason to believe that many insects, and especially bees, see as colours the ultra-violet rays of the spectrum which are invisible to us. Bees show a decided preference for blue colours, butterflies for red and white (the only blue Lepidoptera-flower known is Globularia), but beyond this there is but little colour-preference in insects. Carrion flies go to meat-coloured flowers, but probably because of their carrion smell. We shall probably not be far from the mark if we say that the only preference shown by insects of low organisation is for bright rather than .dull colours (they visit many dull flowers, *e.g.* Adoxa, but it is doubtless the smell that attracts). This being so, it is improbable that the earliest flower-visiting insects had any influence upon the colours of flowers ; they would select the most conspicuous but would not produce any direct effect on colours. We may therefore probably assume that the early flowers were yellow and white, with perhaps a few orange or red species. When the higher forms of insects appeared, there would be a colour-selection and now we can imagine red and blue flowers appearing by the selective action of insects. It may be noted that most blue flowers belong to class H, the rest chiefly to classes B and B′ ; these are the classes visited by bees. Most red flowers are found in class F, and many in B, B′ and H.

Lastly, in this connection mention must be made of the *honey-guides* or pathfinders seen in so many flowers—lines, streaks, or spots pointing to the entrance to the honey, and differently coloured from the rest of the corolla. In Myosotis sp. there is a yellow ring at the mouth of the tube, the

rest of the corolla being blue (this is a classic example, for it was one of C. K. Sprengel's first discoveries; see his *Ent-decktes Geheimniss d. Natur*, or biography in *Nat. Science*, April, 1893); in Pelargonium there are reddish streaks on a pink ground. in Viola light streaks on a deep blue, and so on. These markings as a rule show the way to the honey, and are doubtless useful to visiting insects, and hence, by increasing the rate at which they work, to the flowers themselves, but we must beware of assuming them to be adaptations for this purpose ; they are very likely pheno-mena accompanying changes of colour in flowers, and have been retained as useful characters. [For further details about colour, see Hildebrand, *Die Farben d. Blüthen*, Leipzig, 1879, Müller's *Fertilisation of Flowers*, Wallace's *Darwinism*, &c.]

Whilst conspicuousness and colour are doubtless great attractions to insects, scent is even more powerful, as a consideration of such cases as *Convolvulus arvensis* and *Calystegia sepium* will show, and as is evidenced also by the great number of visitors received by many sweetly-scented and inconspicuous flowers. It is again necessary to re-member the limitation of our own sense of smell, and not to conclude that because we cannot smell it, a flower has no scent. There are several experiments tending to show that bees can smell flowers which to us seem scentless. The carrion smell of such flowers as Arum, Stapelia, &c., repels all visitors but the carrion-loving flies, by which alone these flowers are visited and pollinated.

Of the attractions a flower has to offer in the way of food, honey is the chief. The nectaries are usually at the base of the flower. They may be upon the recep-tacle as in Malva, Compositae, &c., calyx as in Coro-nilla, petals as in Ranunculus, Swertia, &c., stamens as in Cruciferae and Caryophyllaceae, or carpels as in Caltha, Allium, &c. Sometimes they are themselves modified flower-leaves as in Nigella, Aconitum, &c. or parts of them as in Viola. The honey is protected from rain in many ways ; we have considered the chief of these in dealing with the gradual evolution of tubes in flowers. Hairs often serve as extra protections, *e.g.* in the classic example of *Geranium sylvaticum* (see Sprengel, *loc. cit.*), in Malva, Swertia, &c.

The stamens, or parts of them, cover the honey in Campanulaceae, &c., and so on. [See Kerner's *Nat. Hist. of Plants.*] In many plants there is no free honey, but insects (especially bees) bore into certain succulent tissues and suck the sap. Interesting examples are found in Orchis and many other Orchidaceae, Liliaceae (*e.g.* Brodiaea), &c.

Insects, especially small flies, often visit flowers for shelter, chiefly such as hang downwards or have hooded corollas, and in this way a certain amount of pollination is probably effected.

Pollen is an important part of the food of many insects, and was probably the original factor, as we have seen, in starting entomophily. Many flowers depend largely upon it as an attraction at the present day, as much as upon their honey. There exists a class of flowers, **Po** in Müller's classification, which only furnishes pollen to visitors, having no honey. Such flowers are Hypericum sp., Spiraea sp. (*e.g.* common meadow-sweet), Helianthemum, Cytisus sp., Clematis sp., *Rosa canina*, &c. It is in the highest degree improbable that any of these are primitive pollen-flowers; they are probably mostly flowers which have gradually lost their honey-secreting functions. They belong, structurally, to various groups of the honey-flowers, *e.g.* AB and H. They are always, however, in biological work, retained as a separate class; their visitors are mostly flies and pollen-collecting bees. Interesting cases of division of labour among the stamens of a single flower, some providing pollen for insects, some for pollination, occur in Cassia, Heeria, Commelina, &c.

We have seen (p. 64) how the shorter-tongued insects are excluded from the higher types of flower by the formation of tube-structures, and the great morphological importance of this general principle. Various writers, observing these facts, but ignoring the general evolutionary theory of flowers originally proposed by Müller (*Alpenblumen* 1881 ; unfortunately omitted in the English edition of his *Fertilisation of Flowers*), have classed them together with other phenomena under the general heading of "exclusion of unbidden guests." Adding to the fully proved facts of exclusion by tubes, &c. various unproved and more or less fanciful statements[1] about

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[1] *E.g.* the connate water-holding leaves of Dipsacus are explained as an adaptation to keep creeping insects away from the flowers;

the effect of other arrangements in excluding unwelcome visitors, they have caused the whole subject of flowers and insects to fall into disrepute among scientific botanists, and to be regarded as merely an interesting appendage to botany, suitable enough for popular lectures, &c., but valueless in the solution of the important problems of the science. That this is unjust, and that the morphology of the flower cannot be understood except in the light of its natural history, we have endeavoured to indicate above. Morphology must in the long run depend upon physiological study for its elucidation, and experimental physiology must depend very largely upon observational physiology or natural history for the suggestion of lines upon which to work.

Many flowers of high type, with honey at the base of the tube, have their arrangements vitiated by the habit which certain humble-bees (especially *Bombus terrestris*) have of boring holes in the tube, and thus obtaining the honey without pollinating the flowers. Most flowers of the common bell-heathers (Erica) if examined show a perforation at the base of the corolla thus made. If only humble-bees used it, the loss would not be so great, but it is used by hive-bees and wasps also, which do not bore the flowers themselves or only rarely. Other flowers that are, so to speak, circumvented by Bombus, are Aconitum, Dicentra, Lamium, Linaria, Nepeta, Salvia, &c. [For details see Pammel in *Trans. St Louis Acad.*, v.] It is evident that this must be a comparatively recent advance in insect-intelligence, and as yet no signs of a corresponding advance in plant-organisation to meet it have been observed, unless the bladdery calyx of Rhinanthus has been, as some have suggested, acquired to prevent boring; this however is extremely improbable.

If the *time of opening* of the flowers of any species be watched, it will be observed that a few only are open at first, then the number increases to a maximum, and gradually decreases again (in all probability a 'Newtonian curve' would represent the matter; see the next chapter). Now when a species gives rise to a new genus of several species, the evolution as we know goes through the stages of sub-

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similarly the glandular leaves of Pinguicula and other glandular plants. When glandular hairs occur only on the flower-stalk or calyx this very probably is their function.

variety, variety, sub-species, species. If we compare the times of flowering of the varieties of any species, we find their maxima all at or near that of the species itself. Nearly allied species have their maxima more widely separated. If we count up the flowering of a whole genus as we counted that of a species, we find that it too rises to a maximum point at a certain period (it is very likely that this period was that at which the original parent species of the genus had its flowering maximum) and then falls. The same is seen in the natural orders of any single country's flora. Observations on insects give somewhat similar results, and it is found that in general, the proportions of the different biological classes of flowers and insects fairly correspond to one another at different periods.

The bulk of the flowers of the North temperate zone open in summer (maximum in July), but there are many that flower in autumn or early in spring. It is easy to see the advantage to plants of flowering at different periods, especially if they are nearly allied, for the competition for insect-visits is thereby lessened. It must not however be assumed that the phenomenon is an adaptation to this end, many factors influence the flowering of a plant, *e.g.* a check to the vegetative growth. Horticulturists know well that a richly fed plant tends to vegetation rather than to flowering, and the significance of pruning, &c. rests largely on this fact. Plants that are to flower in early spring in temperate climates must have flower-buds laid down the preceding year and also a store of reserve food-materials with which to start growth. Such are Rhododendron, Eranthis, most of our trees, &c. The buds are usually protected by outer scaly leaves, hairs, or other arrangements. A few autumn-flowering plants show similar protections, *e.g.* Hedera, Hamamelis, &c., hence it is very probable that these were once spring-flowerers, but have gradually taken to developing their buds more early. [See MacLeod in *Bot. Jaarb.* v. 1893, and Robertson in *Amer. Nat.* 1895.]

In these spring-flowering plants we have cases, otherwise rare, of protection of flower-buds such as is seen in winter buds of leaves. Xerophytes (see Chap. III.) often show protection of flower-buds against the drought of the dry season. As a rule however the calyx and corolla afford

enough protection to prevent injury by cold, wet, &c. to the more delicate stamens and carpels. In hot tropical regions many flowers are protected against the heat (see Chap. III.).

Many flowers execute protective movements after they have opened; these are chiefly such as expose their pollen very freely to the weather. *E.g.* in Linum, Fragaria, Daucus, Papaver, Anemone, Bellis, &c. the flowers (or heads) curve downwards at night and in wet weather, returning to the erect position in the morning or when it is fine. The flowers (or heads) often close in dull weather or at night, *e.g.* in Anagallis, Bellis, Tragopogon, Calandrinia, and numerous others. Besides these movements there are others which only take place once. The flower-stalks often stand in different positions whilst the flower is in bud to those they occupy when it opens. Hansgirg divides movements of this kind (*gamo-* and *carpo-tropic*) into seven types, *viz.* (1) the Oxalis type, as seen in Oxalis, Geranium sp., &c. (see Pt. II.), (2) the Primula type, as in Primula, many Umbelliferae, &c., (3) the Coronilla type, as in many Papilionate Leguminosae, (4) the Veronica type, as in Veronica, Cardamine, Reseda, Epilobium, &c., (5) the Aloe type, as in Muscari, Funkia, Vicia, Aloe, &c., (6) the Fragaria type, as in Fragaria, Anagallis, Aristolochia, Tussilago, &c., (7) the Aquilegia type, as in Delphinium, Aconitum, Aquilegia, *Solanum nigrum*, &c.

We have pointed out above the general characters of the various biological classes of flowers. We have first the class W, anemophilous flowers; then in entomophilous forms the class Po without honey, and the classes A, AB, B, B', H, and F, with honey. If in any locality the insect visitors to all the flowers be observed, and the number of species of each group visiting all the flowers of each class be recorded, a test of the general flower theory is obtained. A few examples may be quoted from a paper on the British flora (*Ann. of Bot.* 1895). Taking in order the number of visiting species of (*a*) long-tongued bees, (*b*) short-tongued bees, (*c*) Lepidoptera, (*d*) long-tongued flies, (*e*) short-tongued flies, and (*f*) all other insects together, there were found to the 12 flowers of class A the following numbers of visitors:

4; 7, 7, 37; 130, 90; total, 275; average, 23·0;

to the 12 flowers of class B'

43, 16, 49, 90, 120, 59, total, 377, average, 31 5,

to the 25 flowers of class H

49, 7, 21, 28, 30, 20, total, 155, average, 6 2

This shows clearly, especially if it be calculated as per centages, the preferences exhibited by the various insect groups for the flowers whose tube depths are best suited to them The visitors to the flowers of class H are few in number, but by far more industrious than most of the visitors to class A Class B in Britain obtains 'the lion's share of visits—this is explained by the abundance of Compositae in our flora Many authors class together as *allotropous* all the shortest tongued insects (*i e* short tongued flies and all miscellaneous insects) and the corresponding flowers (classes Po, A, AB), as *hemitropous* those insects of medium length tongues (short tongued bees, long tongued flies and all Lepidoptera but the hawk moths) and the flowers of classes B and B', and as *eutropous* the long tongued bees and hawk moths, and the flower classes H and F This is indicated by the semi colons between the figures given above For all flowers observed in Britain the per centages are as follows

Class of Flower	°/₀ of total insect visits	°/₀ of Euti insect visits	°/₀ of Hemitr insect visits	°/₀ of Alloti insect visits
Allotropous	34 7	5 4	21 4	48 7
Hemitropous	50 8	54 6	62 7	43 0
Eutropous	14 4	40 0	15 9	8 3

These percentage numbers give a measure (for the particular region and period of the year) of the attractiveness to insects of the different sorts of flowers The first column shows the attractiveness to insects in general, the others the attractiveness to different groups When a number in one of the latter columns exceeds the one in the first column, it shows a preference by that kind of insect for that kind of flower, thus the hemitropous insects show a great preference for hemitropous flowers (62 7—50 8) and eutropous for eutropous flowers (40 0—14 4)

When a comparison is made, upon the lines just indicated, between the floras of different countries, it is found

that the proportions of the various classes differ a good deal. Thus in the extreme north of Europe eutropous insects are wanting, and there are few eutropous flowers. Those flowers that do occur are found either to have increased vegetative reproduction, or to have shorter tubes enabling the hemitropous visitors to obtain the honey. Thus the insect fauna and its distribution are important factors in determining the geographical distribution of plants. Usually the number of species visiting any one flower that is regularly insect-pollinated is at least two or three and often very many ; if this flower be studied in different countries it will be found visited by different species, but of the same biological class, as regards length of tongue, &c. (*e.g.* short-tongued bees may be replaced by long-tongued flies). There are however a number of cases of mutual adaptation of one particular flower and one particular insect, and in these cases the distribution of the latter regulates that of the former. The best known case is that of Bombus and Aconitum (q.v., and see Bryonia, Angraecum, Yucca, &c.).

Whilst, as we have said, most flowers are visited by all the insects best suited to them and have therefore a considerable variety of visitors, there are numerous cases of more special restriction. Thus the carrion smell and appearance of the flowers of Rafflesia, Stapelia, Ceropegia, Aristolochia, Arum, Helicodiceros and many others causes them to be visited only by carrion-loving (short-tongued) flies; they form a sub-class "carrion-fly flowers." The flowers of Epipactis, Scrophularia, Symphoricarpus, Cotoneaster, &c. are " wasp-flowers "; those of Alocasia, Rohdea, &c. are "snail-flowers"; those of Freycinetia "bat-flowers"; those of Marcgraviaceae, &c. are visited by sun-birds (Old World tropics); those of Erythrina, *Salvia splendens,* Passiflora sp., Abutilon sp. and many more are "humming-bird flowers" (tropics of America). Most of the last-named are bright red flowers, more or less inclined downwards with long tubes, and no landing-places such as occur in insect-flowers. A number of flowers of class F, *e.g. Silene noctiflora, Oenothera biennis, Nicotiana tabacum,* &c. emit their scent only at night, thus attracting night-flying moths. Some of these, and Cereus, &c. only open at night. Such flowers have usually light yellow or white colours. Lastly, mention may be made of the very

special mutual adaptation seen in Yucca, Ficus, Angrae-cum, &c.

Water-pollinated plants are few in number and are all undoubtedly derived from land-plants. Their mechanisms will be treated in Chapter III. (see Water-plants).

The Seed. In all the lower classes of plants the spore (or megaspore) falls out of the sporangium and germinates upon the soil. In the flowering plants proper it remains, as we have seen, in the ovule, and the latter ripens into a *seed* after its ovum has been fertilised. In lower plants the fertilised ovum grows directly into a new plant by continuous growth; in Spermaphytes there is a resting period when the seed is ripe, and growth does not continue until the seed is placed under suitable conditions; given these conditions, it *germinates* or sprouts and the growth into a new plant continues. Most plants (the exceptions are among the lower forms of Algae, and a few Phanerogamic water-plants, &c.) are incapable of movement in their ordinary condition and must live out their life upon the spot where they began it. It is not however advantageous that the offspring should commence life in the immediate shadow of the parent, and we find that at one period of the life-history, every plant is capable of movement from one place to another; this is usually effected in this way that the plant occupies so small a bulk that it is capable of transport by wind or other agency. In the lower forms this 'condensed plant' is the spore, in higher forms the seed. The spore, being of one cell only and thus small and light, is ideally adapted to transport by wind; the seed being necessarily of many cells loses this advantage, but is much more suited to withstand unfavourable conditions of climate, temperature, drought, &c. We find too that many seeds have additional mechanical arrangements for transport from place to place, thus obviating to a great extent the most serious disadvantage under which they labour.

The fertilised ovum gives rise to the *embryo* or young plant contained in the seed. This consists of a short axis, the *hypocotyl*, bearing at its upper end the apical bud of leaves (*plumule*) and one or more seed-leaves or *cotyledons* which do not form part of the bud, but are already comparatively well-developed. At the lower end the hypocotyl

bears the *radicle* or apex of the future root, which faces and is close to the micropyle of the seed. The seed at an early stage consists of integuments, nucellus, embryo-sac, endosperm, and embryo. The embryo-sac with its contained endosperm usually increases at the expense of the nucellus and consumes the whole of the latter tissue. The embryo, meanwhile, treats the endosperm in the same way. The integuments ripen into the *seed-coat* or *testa*. Two cases are to be distinguished in the ripe seed. If the embryo in its growth consumes all the tissue within the seed-coat and comes into uninterrupted contact with it, the seed is *exalbuminous*, or has no endosperm, as in Cruciferae, Compositae, Leguminosae, &c. If there is any tissue within the testa not forming part of the embryo, the seed is *albuminous*. The tissue may be endosperm only, as in Ranunculaceae, Liliaceae, &c.; this is the most common case; or it may be *perisperm* (the nucellar tissue, usually increased by subsequent growth) as in Nymphaeaceae, Piperaceae, &c. Usually there is endosperm as well as perisperm, when the latter is present. The seed must at first depend upon stored food-materials for its growth, until its own vegetative organs are in active order, and so there is always a store of reserves in a seed, either in the embryo (chiefly the cotyledons) or outside it (albumen), or both.

The seed-coat is usually firm and tough, allowing very little evaporation of water from the seed. Its outer cells sometimes have mucilaginous walls and swell when wetted, as in Linum, Plantago, Collomia, Brassica, &c.; sometimes there are scales or hairs upon it and these swell, as in many Acanthaceae. This is usually regarded as a mechanism for attaching the seed to favourable spots for germination. The outer layer of the testa becomes fleshy in Bixa, Magnolia, Moraea, Cycas, &c. (see below), and it is sometimes provided with hooks or wings, and often with hairs.

Many seeds have an extra coat covering them, which is developed like the original integuments, *i.e.* by a cup-like growth of tissue around the seed from the top of the stalk or rarely from the micropyle. This structure is called an *aril*. Its development may be studied in fruits of Euonymus. Arillate seeds occur in Taxus, many Commelinaceae, &c., Dilleniaceae, Celastraceae, Sapindaceae,

Passiflora, Nymphaeaceae, Myristica, &c. In Euphorbiaceae, &c. the aril remains small and hard and is called a *caruncle*, but usually it is fleshy.

The seed may be ana-, campylo-, or ortho-tropous, as was the original ovule (p. 79); the embryo may be straight, curved, twisted, &c.; the endosperm may be *farinaceous*, *floury*, or *mealy* (the cells containing starch and when powdered forming a floury dust) as in Triticum, *oily* as in Papaver, Ricinus, &c., *fleshy* as in Berberis, *horny* as in Coffea, *bony* as in Phoenix and Phytelephas, *ruminate* (marked by transverse lines which give it a marbled look) as in Anonaceae. The embryo may have one, two, or several cotyledons (this is an important point in classification), or rarely none, as in Cuscuta, &c.

Mention must be made, lastly, of the *adventitious* embryos of Funkia, Nothoscordum, Alchornea, &c. and of the peculiar cases of Ginkgo, and Gnetum, where the seed 'ripens' before fertilisation; see Pt. II.

The Fruit. The ovule is usually enclosed in an ovary, or protected by scales as in Coniferae, and these parts are stimulated to further growth by the act of fertilisation and develope together with the ripening seed, finally forming a covering or protection to it, known as the *fruit*. The fruit may be defined as 'the product of that process of growth which is initiated by the act of fertilisation.' This of course includes the seed, and in Cycas, Taxus, &c. fruit and seed are the same. Usually, however, the seed is enclosed in an envelope or *pericarp*, developed from the gynœceum, &c. Most of the text-books lay stress on the difference between *true* fruits and *false* fruits (*pseudocarps*), the former being defined as the product of the ovary only, the latter as the product of the ovary together with any other organ that developes, such as the axis or perianth. The terms, however, are most inconsistently used, and we shall avoid them here.

Fruits may be divided first of all into *simple, aggregate*, and *multiple*. Where a flower gives one indivisible fruit, the fruit is simple, as in cherry or oak; where it gives several similar fruits, independent of one another, as in raspberry, buttercup, Ochna, &c. the fruit is aggregate; where several flowers combine to give one fruit, as in mulberry, fig, plane,

&c. the fruit is multiple. In description, mention is made of the multiple or aggregate nature of the fruit and then one of the units is described as if it were a simple fruit.

Fruits may be *dry* or *fleshy*; they may open to allow the seeds to escape (*i.e.* may be *dehiscent*) or may remain closed (*indehiscent*). Indehiscent dry fruits are usually one-seeded, as it would be a disadvantage to have many seeds germinating near together. Fleshy fruits rarely dehisce, as they are eaten by animals and the seeds are thus separated. Some dry fruits break up into one-seeded portions (usually corresponding to the individual carpels); these are termed *schizocarps* and the portions *mericarps*.

We shall now give a brief classification of the chief kinds of fruit, with a few examples of each.

Dry Fruits. The indehiscent forms are divided into two main groups, *achenes* and *nuts*. The former is usually defined as the product of one carpel, the latter as that of more than one, but in practice all small seed-like one-seeded dry indehiscent fruits are achenes, all large ones nuts. True achenes are found in Ranunculus, Potentilla, &c. but the name is also given to the fruit of Compositae, Gramineae (this variety, with pericarp and testa united, is sometimes called a *caryopsis*), Labiatae, &c. True nuts, from superior ovaries, occur in Betulaceae, but the term is applied to the large one-carpelled fruit of Anacardium, &c. A variety of either achene or nut is the *samara* or winged one-seeded indehiscent fruit, seen in ash, elm, Banisteria, Liriodendron, Ptelea, Ventilago, Seguieria, &c.

Schizocarps are of various kinds, *e.g.* the *lomentum* of many Leguminosae (a pod that is constricted between the seeds and breaks into one-seeded portions), the schizocarps of Euphorbiaceae, Geraniaceae, Malpighiaceae, Umbelliferae, many Malvaceae, and Sapindaceae, &c.

Dry dehiscent fruits are of several kinds; the most common are the *follicle, legume,* and *capsule.* The follicle consists of one carpel, and dehisces along the ventral side only, as in Aconitum, Asclepiadaceae, Apocynaceae, Crassulaceae. The legume is similar but dehisces along both sides, as in most Leguminosae (a pea-pod is a typical legume). All fruits of more than one carpel are grouped under the general name of capsule, but special forms have special names, *e.g.* the

pod-like *siliqua* of Cruciferae, &c., the *pyxis* of Anagallis, &c. (capsule opening by a lid), and others. The way in which the ordinary capsule dehisces is often of systematic importance. The general method is by splitting from the apex towards the base. If the splits, as in Iris, Epilobium, &c. run down the midrib of each carpel, the dehiscence is *loculicidal*: if, as in Hypericum, the fruit breaks into its component carpels, leaving the placental axis standing, it is *septicidal*; if the outer wall of the fruit breaks away, leaving the septa standing, it is *septifragal*.

Fleshy Fruits. The commonest types are the *berry* and *drupe*. The former contains no hard part but the seeds; these are surrounded by fleshy tissue and there is a firmer skin (*epicarp*) on the outside. Berries may be derived from superior ovaries, as in Berberis, Vitis, Solanum, &c. or from inferior, as in Ribes, Vaccinium, &c. In rare cases the berry dehisces, as in Myristica and Akebia, or is constricted between the seeds, as in Unona and Maerua. The drupe (*e.g.* cherry) has a skin (*epicarp*) on the surface, then a fleshy mass of tissue (*mesocarp*) and a hard shell or stone (*endocarp*), all forming part of the pericarp; within the stone is the seed or kernel, usually without a hard coat. Drupes from superior ovaries occur in Prunus, &c., from inferior in Cornaceae, Juglans, &c. There may be one stone (Prunus) or several (Cornus). Other fleshy fruits are the *pome* of Pyrus, &c. in which the fleshy receptacle encloses, and is united to, the core or product of the gynœceum proper ; the *pepo* or gourd of Cucurbitaceae (*e.g.* cucumber) a variety of the berry with hard epicarp, the peculiar pseudo-berry of Juniperus (q.v.), &c., the fruit of strawberry (large fleshy receptacle bearing achenes), rose (fleshy receptacle enclosing achenes), Anacardium (fleshy receptacle bearing a nut), Gaultheria (a capsule enclosed in the fleshy calyx), Urera, &c. (achene in fleshy perianth), and so on. Aggregate fleshy fruits occur in Rubus (drupes), Anonaceae (berries), &c. Multiple fleshy fruits are frequent in Moraceae (*e.g.* mulberry, fig, bread-fruit), Ananas, Carludovica, Anona, &c.

Other interesting morphological features in fruits are mentioned below. Reference for details should be made to Pt. II.; besides the families and genera mentioned see Aesculus, Bertholletia, Chenopodium, Leontodon, Nymphaea-

ceae, Nyctaginaceae, Palmae (*e.g.* Phytelephas, Lodoicea, &c.), Pandanaceae, &c.

Distribution of Seeds. A consideration of the ways in which seeds are dispersed to a distance from the parent plant is of importance in two ways. In the first place it helps us to an understanding of many questions in the geographical distribution of plants, such as the planting of oceanic islands, the presence of stray plants from one flora in the midst of an alien flora, and so on. In the second place it is a very important factor in the life-history of an individual plant or species. It is evidently advantageous to a species that the seeds of its members should be carried to a little distance from the parent plant and from one another, so as to avoid shading by the parent and excessive mutual competition. From the first consideration it behoves us to examine all *occasional* means of seed-transport, *i.e.* all means by which seeds can by any possibility be dispersed. In the life-history of the individual, on the other hand, only *regular* means of transport, *i.e.* such as regularly take place by aid of special mechanisms in the seed or plant itself, are of any importance.

One great obstacle to migration of species is a wide extent of ocean. Many seeds however are found to be able to withstand sea-water for sufficient periods to be carried long distances. Trunks of trees may be floated away, carrying earth and seeds with them. Numbers of seeds, capable of germination, are thrown ashore in Western Europe, having been brought by the Gulf Stream from the West Indies. Floating ice, especially river-ice, may also prove important in carrying seeds. Tornados frequently carry seeds, &c. to great distances, though they may not be adapted to ordinary wind-carriage. The balls of mud carried on the feet of water-birds, partridges, &c., often contain seeds in good condition. Carnivorous birds sometimes swallow their prey and afterwards void the contents of its crop, containing seeds capable of germination. Locusts carry grass-seeds with them, and so on (see *Origin of Species*, Ch. XII.).

Turning now to the regular methods of seed-dispersal, we find four agents that may be employed for the purpose —wind, water, animals, and propulsive mechanisms upon the parent plant itself.

For wind-carriage the simplest arrangement is for the parts to be carried to be light enough to float in the air like dust. The unicellular spores of ferns, &c. fulfil this condition. The nearest approach to it in seed-plants is in the Orchidaceae, whose seeds are extremely small and light. Pyrola and many Caryophyllaceae, &c., have also very light seeds. A number of plants with dry fruits have what may be termed 'censer' mechanisms. The fruit opens so far as to leave the seeds room to escape, but opens in such a way that they can only escape when the fruit is violently shaken, *i.e.* as a rule, only when a strong wind is blowing; the seeds thus escape at a time when they have a good chance of being carried some distance. Such fruits are the capsules of most Liliaceae, Iridaceae, Caryophyllaceae, &c., the fruits of Aconitum, Helianthus, &c. The seeds are liable to damage from rain in an open fruit of this kind; some close when it rains, others only open by narrow protected openings, *e.g.* Papaver, Campanula. In Tulipa, Iris, &c., the seeds are flattened, thus increasing the surface exposed to the air without increasing their weight. In Pinus, Deutzia, Gordonia, Zanonia, Millingtonia, &c., the seed is winged as well as more or less flattened, and may be carried to some distance before reaching the ground. In Fraxinus, Liriodendron, Acer, many Malpighiaceae, Serjania, Seguieria, Ptelea, Ulmus, Paliurus, Ventilago, Abronia, Tripteris, Terminalia, Pterocarpus, Centrolobium, &c., the wings are on the fruit, outgrowths of the pericarp. In Bougainvillea, Spinacia, Mirabilis, Carpinus, &c., the bracts or bracteoles form the wings, in Triplaris, Armeria, Davilla, Rumex, Dipterocarpaceae, Trifolium sp., &c., the perianth, or part of it. In *Rhus Cotinus*, Spinifex, &c., the fruit-head is rolled bodily about by the wind (cf. Selaginella sp.); it is usually stated that the whole plant of Anastatica is rolled about, but recent observations throw doubt on this. Lastly, a great number of seeds and fruits exhibit very perfect 'parachute' mechanisms in the form of tufts or coverings of hairs. Such are the seeds of Salix, Gossypium, Epilobium, many Apocynaceae and Asclepiadaceae, Aeschynanthus, &c.; the achene fruits of Eriophorum, Typha, Anemone, Compositae, &c.; in Clematis the style becomes hairy after fertilisation.

Adaptations in the structure of the fruit or seed to water-carriage are found in a few water-plants (Chap. III.), and in Veronica sp., &c.

Animal distribution is of two kinds--inside or outside the animal. To the former class belong all fleshy fruits; these are eaten and the seeds afterwards dropped. It is obviously necessary that the seeds should be able to pass uninjured through the alimentary canal. This is usually effected by means of a hard covering, the seed-coat in berries, the endocarp in drupes. In some cases the seed is sticky, *e.g.* in Viscum, and is ejected by the bird; in Strychnos, &c., it is poisonous. Most fleshy fruits are distributed by birds and are found on shrubs and trees; comparatively few are eaten by other animals. They are commonly brightly coloured when ripe, so as to attract notice (cf. flowers). In Anthurium, Magnolia, Acacia sp., &c., special arrangements for increasing the conspicuousness are found. The seeds of Abrus, Adenanthera, Ricinus, &c., and the fruits of Scorpiurus, Biserrula, &c., resemble beetles or caterpillars, and it is often suggested that birds are deceived by them and carry them to a distance before finding out the mistake. Turning now to carriage of seeds or fruits by the outer surface of the animal's body, this is usually effected by hooks upon the seed or fruit. Such cases may be classed under the general name of burrs. Hooked seeds are very rare; they occur in Villarsia, &c. Hooked fruits are common; the hooks may be on any part of the fruit proper or on the accessory organs—receptacle, corolla, &c. (*e.g.* cf. Bidens, Tragoceros, and Xanthium, in Compositae). Examples are Triglochin, Uncinia, Cenchrus, Emex, Triumfetta, Bunias, Agrimonia, Acaena, Geum, Medicago, Circaea, Blumenbachia, Sanicula, Daucus, Galium, Asperula, Cynoglossum, Martynia, &c. In Tribulus, &c., the fruit has hard spines and lies upon the soil till trodden on by an animal and is then carried away sticking in its foot. The most formidable fruit of this kind is Harpago-phytum. In Arctium the hooks cling to passing animals and finally let go their hold and the plant swings back jerking out the fruits. In Allionia, Pisonia, Plumbago, Siegesbeckia, &c., the fruit clings to animals by means of glandular hairs.

Lastly we come to those cases in which there is a propulsive mechanism in the fruit itself. This may be one of two kinds. In Dorstenia, Oxalis, Impatiens, Cyclanthera, Ecballium, &c., the propulsion depends upon extreme turgidity in some part of the fruit. In Lupinus, Ulex, Eschscholtzia, Scandix, Euphorbia, Ricinus, Hura, Acanthaceae, Alstroemeria, Cardamine, Buxus, Claytonia, Viola, Geranium, &c., tensions are set up by the drying of certain parts of the fruit-tissue when exposed to the air.

Observation shows that as a rule none of the mechanisms found upon seeds or fruits transport them to great distances; a few hundred yards is usually the maximum. This, however, is probably as much as is necessary to gain all the advantages of seed-dispersal.

Fruits usually only open in dry air, and remain closed protecting the seeds, in moist air. Exceptions to this rule occur in xerophytes (Chap. III.), where protection is rather needed against drought than damp. Colchicum and other autumnal plants protect their fruit during the winter by keeping it below the soil. In Arachis, Voandzeia, Trigonella sp., Amphicarpaea, Cardamine sp., &c., the plant produces subterranean fruits, either from subterranean or subaerial flowers. In Erodium, Stipa, &c., the fruit has a self-burying mechanism. Reference may also be made to Linaria, Cyclamen, &c. The fruit of Anthemis sp., and many seeds (p. 105) have outer layers of mucilaginous cells, &c., which swell when wetted and anchor them to the soil.

In studying the mechanisms of seed-dispersal, the morphology of the various fruits should be compared. It is of interest to notice how in different fruits the same end is attained in different ways; *e.g.* how the testa, aril, gynœceum wall, receptacle, corolla or perianth may be fleshy, or hooked, &c. It should also be noted that there is much greater variety in this respect among nearly allied forms than there is in the general floral mechanism. This goes to show that the seed-dispersal methods are of recent acquirement. Such orders as Cruciferae, Compositae, Leguminosae, Rosaceae, Umbelliferae, and such genera as Trifolium, Valerianella, &c., are of special interest in this connection. Further details will be found in Pt. II., and in Chap. III. (especially see under Epiphytes). The standard work on the subject

is Hildebrand's *Verbreitungsmittel d. Pflanzen* (Leipzig, 1873); reference may also be made to Kerner's *Nat. History of Plants*, the *Origin of Species*, &c. The literature to 1890 is indexed by MacLeod in *Bot. Jaarbock*, Gent, 1891.

Germination. Placed under suitable conditions—darkness, moisture, supply of oxygen, and suitable temperature—the seed germinates. The testa is burst by the swelling of the seed, the radicle is pushed out, at or near the micropyle, by the lengthening of the hypocotyl, and grows down into the soil as the root. The plumule presently comes above ground, often bent back on itself into a hook-shape (as seen in sprouting peas), and begins to develope into the young shoot. The cotyledons as a rule come up too, turn green, and act as the first foliage leaves, but if there is any endosperm they first of all act as absorbent organs to take up the reserves it contains. In a few exalbuminous seeds, *e.g.* pea, the cotyledons are so gorged with reserves that by the time they are exhausted the young plant is well enough grown to be independent, and there is no need for them to turn green, nor do they. Such also is the case in a few albuminous seeds, *e.g.* the Gramineae.

Observations have been made (see Detmer's *Keimungs-physiologie*) on the heights, weights, &c., of plants grown from heavy and light seeds, and they show that, other things being equal, the offspring of the former are as superior to the latter as the offspring of cross- to that of self-fertilisation, so that a very important factor in life-histories turns up here. It might well pay a plant, so to speak, to give up cross-fertilisation and expend the saving on heavier seed or on more numerous seed. Of course, as usual, a balance must be struck between opposing necessities; the heavier the seed the less its chance of distribution.

Another interesting point that is frequently seen in seedlings is the exhibition of transitional stages towards the mature state (see Acacia). This may be seen in many plants which when mature differ in morphological habit from their related forms. It is a case of the well-known so-called Law of Recapitulation that "the development of the individual recapitulates the development of the race." This

w. 8

is probably true in a general sense, but not in detail; secondary characters (adaptive) are liable to confuse the matter. Good examples are Acacia, Bossiaea, Ulex, Hakea, many succulents, &c.

Vegetative Reproduction. It frequently happens that portions of the vegetative organs, specialised in structure or not, are detached from the plant and grow into new plants. This process is termed vegetative reproduction, and is one of great importance, both in the individual life-history and to the species collectively. The detachment from the parent need not necessarily precede the growth of the new plant, but may follow it, as in the case of the young strawberry-plants formed upon the runners. It is of interest to notice the various ways in which the young daughter-plants may be nourished. If the detached portion of the parent be not green, as *e.g.* a potato tuber, a supply of reserve materials must be stored up in it to start its growth and keep it growing until it can assimilate for itself, so that it is the physiological though not the morphological equivalent of a seed (gardeners speak of 'seed-potatoes'). If the young plant, as *e.g.* in the strawberry, remain in connection with the parent, no reserves are needed, the parent feeding it till it is capable of independent existence.

Vegetative reproduction is very certain, effective, and economical; the profusion of such plants as daisies, buttercups, raspberries, hyacinths, &c., is largely due to it. Its chief disadvantage is the loss of the benefits due to fertilisation (p. 47); those connected with seed-formation, *viz.* protection of the plant during the unfavourable period of the year, and dispersal of the offspring, are obviated in various ways (see below). The young plants start at a considerable advantage as compared with seedlings, having such a large supply of food-materials to draw upon.

It is well-known that in a sense the vegetative and 'true' reproductive activities of a plant are antagonistic (see p. 100). If a plant is growing in rich soil or in the shade, the vegetative activity is favoured, whereas when vegetative growth is checked, the plant tends to flower more. In plants that possess modes of vegetative reproduction, excessive vegetative activity tends to favour this method of propagation at the expense of the sexual method. Vöchting (*Prings.*

Jahrb. 1893) has shown by direct experiment that reduced light favours vegetative multiplication.

As we have seen, it is a very rare occurrence for the root ever to give rise to a shoot, and so vegetative reproduction generally consists in the detachment of a shoot-structure, with or without roots. As might be expected, it is almost confined to herbaceous plants; comparatively few trees are thus propagated. We shall give a brief sketch of some of the more common methods of vegetative reproduction here; for further details see Chap. III. and Pt. II.

Propagation by the simple detachment of a branch from the parent plant, not in any way modified in structure, is common in water-plants, and in plants with rhizomes. Special branches for vegetative propagation are the runners of Fragaria, Ranunculus, Agropyron, Ajuga, Nephrolepis, &c., the suckers of Gesneriaceae, Epilobium, Rubus, Agave, Sempervivum, Salicaceae, &c. Bulbs, corms, tubers, &c. all lend themselves readily to this mode of propagation; all these are dealt with in Chap. III. Similar structures appear above ground in many plants, and are then primarily reproductive; such are the *bulbils* or little bulbs of Lycopodium, Agave, Lilium, Allium, Remusatia, Gagea, Dentaria, Oxalis, &c. (these usually appear in place of flowers, in the inflorescence), the tubers of Begonia, Globba, Polygonum, &c., the young plants that appear by budding of tissues in Asplenium, Cardamine, Bertolonia, Begonia, Rubus, Chlorophytum, Crassula, Sinningia, &c.

The disadvantageous tendency in vegetative multiplication is that the offspring shall be so closely crowded together as to cause a severe competition between themselves and between them and the parent plant. To avoid this danger in seed-reproduction, there are several methods, as we have seen, and the same is the case here. In water-plants the detached branches or buds are carried away by the water. Many detached parts are carried off by birds for nest-making, *e.g.* in *Tillandsia usneoides;* others have arrangements for adhering to animals, *e.g.* the hooked bulbils of Remusatia, the branches of Mammillaria, &c. The nodes of Panicum and other grasses pass through the alimentary canals of animals and subsequently germinate. The tubers of *Senecio articulata* may be rolled along the ground by the wind,

like the plants of *Selaginella lepidophylla*. The bulbils that so frequently occur in inflorescences may be jerked to a distance when the plant is shaken. When the reproduction is by suckers, runners, or similar methods, the length of these is usually sufficient to ensure separation of the offspring from one another and from the parent.

Appendix. Hairs, Emergences, Latex, &c. A few minor anatomical features remain to be mentioned, as they are sometimes of importance in classification, natural history, &c.

Hairs are cellular outgrowths from the epidermal tissue, branched or unbranched, of the most various shapes, and are exceedingly common on all parts of plants (for descriptive terms see p. 28). Their use is often doubtful, but in many cases we can see what it is. Thus the dense hairy covering of many xerophytes checks transpiration, the stinging hairs of Urticaceae, Loasaceae, &c., are protective, the barbed hairs of the fruits of Galium, Blumenbachia, &c., serve for animal distribution, and so on.

Emergences are outgrowths of the surface which arise from other tissues as well as the epidermis, *i.e.* are partly endogenous in origin (p. 22). Such are the tentacles of Drosera, which contain vascular bundles, the prickles of Rosa and Ribes, and other such outgrowths.

Latex is a milky fluid, usually white or yellow, contained in special *laticiferous vessels* or *cells* which run through the tissues of certain plants, *e.g.* Euphorbia, Cichorieae (Compositae), many Papaveraceae, Apocynaceae, Asclepiadaceae, Sapotaceae, &c. The fluid contains substances of various kinds; some are of use in the nutrition of the plant, and to some extent the laticiferous tissue therefore replaces the phloem; others, *e.g.* caoutchouc, are apparently excretory products of little or no use to the plant.

Raphides are needle-shaped crystals of calcium oxalate, contained in the cells, especially in young growing parts and in Monocotyledons. The painful effects of chewing a piece of the leaf of *Arum maculatum* are due to the raphides sticking into the mucous membrane.

Water-pores or *hydathodes* are openings, resembling stomata, upon leaves or elsewhere, through which the plant excretes water, often containing other substances, *e.g.* chalk,

in solution. During the day evaporation carries off the water, but at night it often accumulates and is generally mistaken for dew. The drops of water so commonly seen in the morning on the tips of grass blades have been thus formed. Water-pores are also found in many species of Saxifraga, Tropaeolum, Fuchsia, Caladium, &c. When the water contains sugar in solution, a nectary (p. 62) is formed[1]. These are usually in flowers, but there are many cases of *extra-floral* nectaries, *e.g.* on the leaves of the cherry-laurel (Prunus), stipules of Vicia, Viola, &c. Extra-floral nectaries usually attract ants in large numbers, and this brings to the plant a certain advantage by keeping off caterpillars, &c. Several tropical plants show extreme cases of adaptation in this direction, by housing and feeding standing armies of fighting ants. Such plants are said to be *myrmecophilous* (see Acacia, Cecropia, &c.). In this connection mention may be made of the *honey-dew* so common on leaves (see Acer, Pithecolobium, &c.), and of the *domatia* or little dwellings inhabited by mites, usually constructed of hairs, or sometimes in little hollows or grooves of the leaf (see Ludwig's *Biologie*).

Resin-passages are large canal-like intercellular spaces in the tissues of certain plants, *e.g.* Coniferae. Into them the plant secretes resin; this appears to be a waste-product, though it may have an incidental value in protecting the wood from decay, or in other ways.

Oil-cavities, containing oils of various sorts, are frequent in various plants, especially in the leaves, where they show as translucent dots when held up to the light. They occur in Rutaceae, Guttiferae, &c.

The treatment of morphology &c. given in this chapter and chapter III. will suffice for most purposes. Advanced students should consult original papers and special books for details or discussions of certain points. A few of the more important are:

Morphology: Asa Gray's *Structural Botany;* Eichler's *Bluthendia-gramme* (Leipzig, 1878); Goebel's *Outlines of Classification and Special Morphology,* and his *Entwicklungsgeschichte des Pflanzenorgane* (in Schenk's *Handbuch der Botanik*); K. Schumann's *Morphologische Studien* and *Neue Untersuchungen uber die Blütenanschluss;* Campbell's *Mosses and Ferns* (London, 1895); Bower's *Studies in the Morphology of*

[1] Usually there is no pore in a nectary, the fluid being excreted by the superficial cells.

Spore-producing Members (*Phil. Trans.*, recent years), and others of his papers; Goebel's *Pflanzenbiologische Schilderungen* and papers in *Flora* &c.

Natural history: the best general paper on the flower is that of MacLeod in *Bot. Jaarboek*, v, Gent, 1893 (Dutch); others are Loew's *Einleitung in die Blütenbiologie* (Berlin, 1895) and his *Blütenbiologische Floristik* (Stuttgart, 1894), which gives a résumé of all work upon the European flora; indexes to the literature are given (to 1883) in Müller's *Fertilisation of Flowers* (London, 1883; a useful book for facts, but out-of-date in its generalisations), (to 1889) by MacLeod in *Bot. Jaarboek*, Gent, II, 1890, (to 1894) in Loew's *Floristik:* the fruit and seed are dealt with in Hildebrand's *Verbreitungsmittel der Pflanzen* (Leipzig, 1873), and the literature to 1890 is indexed in *Bot. Jaarboek*, 1891: other classical works are Darwin's *Cross and Self Fertilisation, Forms of Flowers, Fertilisation of Orchids, Origin of Species,* &c., and Sprengel's *Entdeckte Geheimniss der Natur* (reprinted Berlin, 1894), &c.

Other papers &c. are referred to in the text.

CHAPTER II.

VARIATION, EVOLUTION, CLASSIFICATION.

THE account of evolution here given is not intended as anything more than a sketch, to indicate its bearing upon the principles of classification. Into the discussions as to the precise mechanism of evolution we shall not enter, but shall merely give a short outline of the main points of the theory as enunciated by Darwin.

Rate of Increase. Every species of animal and plant, even the most slow-breeding and least prolific, produces so many offspring that if nothing interfered with their subsequent growth and propagation they would soon cover the entire surface of the globe. As the average number of representatives of each species remains fairly constant from year to year, it is evident that a vast amount of destruction must take place, and that only a few of the offspring of each generation survive. The destruction is greater in the case of such organisms as codfish or orchids than in the case of such as elephants or labiates, but in all cases there is destruction, more offspring being produced than can possibly survive to propagate their kind. It is important to remember that only those organisms which do this are of any serious importance in the general history of the species.

The destruction of the extra number of individuals in each generation is effected by many agencies—animal enemies, parasitic enemies, competition with other individuals of the same or different species, unfavourable conditions of climate or environment, &c. When a species

is transferred to a new country the balance that existed in its former habitat between its rates of increase and destruction is interfered with. The interference is often in a favourable direction, as is illustrated by the extraordinary multiplication of rabbits in Australia, of Elodea in Britain, of thistles and cardoons on the Pampas, of cacti in South Africa, and so on. On the other hand many species are unable to establish themselves in new countries, even though, as far as we can judge, the conditions of life are as favourable as in their old localities.

Struggle for Existence. It follows from what we have said that there must be among plants and animals a continual struggle for existence and propagation, both against one another and against the external conditions of life. The struggle will be keener between individuals of the same species than between those of different species, but will occur wherever individuals are so close together as to compete for soil, light, air, or other necessaries. There may even be competition between plants miles apart, as we have seen on p. 83, for the services of insects. In deserts, arctic countries, and similar situations, the struggle is rather between plant and climate or environment, than between plant and plant, as the individuals are not usually very close together. In all cases however an organism has to undergo a severe struggle to maintain its existence and propagate its kind.

We have now to consider what it is that determines which individuals are to survive, or whether a given individual shall succeed or perish. If every individual were exactly like every other one of the same species, the determination would be 'accidental'; those organisms which happened to be under the most favourable conditions would be the survivors. The question however is not so simple as this, for the individuals of a species are by no means all alike; some for example are perhaps the offspring of cross-, others of self-fertilisation, in which case the former will win in the struggle, other things being equal; or again some may spring from heavy, some from light seeds (p. 113) and so on. Apart from this there is also much variety in character among the different individuals, and we must now deal with this feature.

Variation. That no two organisms are exactly alike, even though they be the offspring of the same parent, is a well-established fact. Whatever character be chosen, examination of a large number of cases will show that it is not uniform in all but varies in its degree of development in different individuals. The study of variation has received much less attention than it deserves, considering that upon it rests the whole theory of evolution; recently however several important pieces of work have been done in this direction.

To formulate laws of variation in the present state of our knowledge is almost impossible; we shall only give in this place a sketch of a few of the important and well-established generalisations that have been made.

If we study any character whose value can be numerically expressed, *e.g.* the height of the individual, the number of seeds produced, the length of the tube in the flower, &c., it is found that if a sufficiently large number of individuals be measured, the amount and nature of the variations can be expressed by a simple curve, variously known as a Newtonian, Galtonian or binomial curve. This curve is similar in shape to that which represents the effect of temperature on growth (p. 41), rising from zero to a maximum and falling off again to zero on the other side. Thus the lengths of the lowest fruits of 568 plants of *Œnothera lamarckiana* were measured by De Vries with the following result:

Length of fruit in mm.	15	16	17	18	19	20	21	22	23.
Number of individuals	1	1	5	11	17	27	37	62	74.
Length	24	25	26	27	28	29	30	31	32	33	34.
Number	83	79	51	43	32	18	13	5	5	3	1.

The maximum number of fruits thus have a length of 24 mm., midway between the two extremes. The larger the number of individuals measured, the more closely does the curve approximate to the true binomial curve.

Similar results are obtained by counting the numbers of ray florets in the Compositae; thus in *Chrysanthemum leucanthemum* (ox-eye) the maximum number of heads have 21 ray florets, in *Anthemis cotula* 13, and so on. It will be noticed that these are two of the numbers of the phyllotaxy series (p. 37), and in counting the ray-florets one usually finds secondary maxima at the other numbers of

this series, *e.g.* if the chief maximum be at 13, there may be secondary ones at 8 and 21.

In some cases the variations are all on one side of the maximum, and we obtain what have been called "half Galton curves." Thus countings of the perianth in *Caltha palustris* by De Vries gave the following result :

| No. of leaves | 5 | 6 | 7 | 8. |
| °/₀ of individuals | 72 | 21 | 6 | 1. |

By cultivation and selection De Vries succeeded in producing races of buttercups in which the variation was symmetrical about the numbers 9 and 10 petals, starting from one in which it was asymmetric about 5, like Caltha. Into the details of the use of these curves in the study of variation, &c. (*e.g.* in determining whether a given community is a pure race or a mixed one) we cannot here enter. [See Literature at end of chapter.]

Whilst, in general, variation is *continuous, i.e.* there are all possible intermediate steps between the two extremes, this is by no means universally the case. Variation is often *discontinuous,* one or more individuals appearing with a variation not connected by intermediate steps with the other individuals of the species. Such variations are termed *sports,* and if they be of a very pronounced nature may be *monstrosities.* Monstrosities graduate into sports by easy stages and it is difficult sometimes to decide under which head to class a given variation. The study of monstrosities is termed *teratology,* and was formerly much employed in the decision of morphological problems. Thus the frequent occurrence of green leaves in place of carpels was regarded as a proof of the derivation of the latter from leaves, the doubling of a flower (*i.e.* the change of its stamens into petals) as a proof of the derivation of stamens from petals (see p. 62), and so on. Other common monstrosities are *fasciation,* often found in buttercups, &c. and hereditary in the garden cockscomb (Celosia, *q. v.*), in which the stems and branches are laterally united, forming a flat structure, and *prolification,* or formation of buds in the axils of floral leaves. The evidence of monstrosities can only be regarded as useful in solving morphological problems when a series of stages can be found between the monstrous and the normal forms.

We must now go on to consider a few other generalisations that have been made from the observed facts of variation. It is found by experience, for example, that the species of large genera vary more than those of small. In the British flora, a comparison of the species of Rubus, Salix, or Potamogeton with those of Agrimonia, Betula, or Ceratophyllum will illustrate this fact. Again, those species which are widely-ranging, diffused and common vary more than those which are less marked in these characters, other things being equal. To take an example from our own flora, *Rosa canina* should be compared with the less common species of Rosa, or *Rubus fruticosus* with *R. Chamaemorus.*

In any organism it seems a general rule that multiple, rudimentary, or lowly-organised structures are variable. Thus the stamens vary much in flowers such as those of Ranunculaceae or Rosaceae, where they are usually described by systematists as 'indefinite.' The rudimentary gynœceum of male flowers (*e.g.* Rhamnus), or andrœceum of female flowers (*e.g.* Nepeta, Araceae, &c.), is a very variable structure. Or again, more variation may be seen in the corolla of polypetalous flowers than in the more highly organised corolla of the Sympetalae.

A very important factor in variation problems is what is termed *correlated variation*. By this is meant that when an organism varies in one part, the result is usually a variation in other parts as well, often such as have apparently no direct relationship to the first. Very probably nutrition has a great deal to do with this. If we could measure the green area in a number of plants of the same species, we should doubtless find that there was a mean size of plant possessed by the maximum number of individuals, as already explained. Now the amount of assimilation will depend upon this area and upon the total amount of light (of sufficient intensity) falling upon it. In general, then, the amount of available food material in the plant will be fixed by these conditions, and if an extra amount is diverted into any channel, as will happen in many cases of variation, the balance will have to be redressed elsewhere, and this may be the cause of further variations. No rules can be formulated about variation of this kind, but there are many cases which seem only explicable by assuming correlation.

Natural Selection. If there were no variation among the individuals of a species, there would be, as we have seen, a 'survival of the accidentally favoured.' When however variation enters into the problem as a factor, the result is entirely different. Those individuals which possess any superiority over their fellows in any character which is of importance in the general conditions of life, will on the whole be the survivors, and there will thus be what may be termed a 'survival of the fittest,' or a 'natural selection,' analogous to the artificial selection employed by breeders, who select in each generation the finest and most suitable individuals to propagate their race. Of course the survival of accidentally favoured individuals will also occur, but in the long run the effect of this factor will be *nil*, as it will sometimes select better, sometimes worse, individuals. The importance to an animal or plant of even a slight variation can only be appreciated after considerable familiarity with outdoor natural history has been attained, and even then only in a few cases. The very delicate adjustment of the balance subsisting between the various organisms of a district and between them and their surroundings may be disturbed even by the most apparently trivial causes. We know for instance that the length of the tube of the flower in a given species is variable; now we have seen (pp. 64, 101) that upon this length largely depends the composition of the group of insect-visitors, the longer-tubed flower excluding more of the shorter-tongued insects. Hence the longer-tongued visitors will find more honey and therefore spend more time in such a flower, and will thus probably become better coated with pollen, or better pollinate the stigmas, as the case may be. The result will therefore tend on the whole to be that the longer-tubed flowers will set more seed than the shorter-tubed, and thus, as the offspring inherit the parental characters, that the length of the flower tube in the species will tend to increase. This may go on until a further increase becomes disadvantageous, and then any flowers whose tubes are too long will tend to be eliminated as well as those whose tubes are too short, whilst those whose tubes are of the best possible length will succeed best. The result of this will probably be, therefore, that the range of variation in tube-length will gradually tend to diminish,

though still forming a symmetrical curve about the optimum length, and we may say that the character is becoming 'fixed.' Numerous similar illustrations might be given, but it is sufficient to have called attention to the important fact that we must not without proof regard any variation as of no importance to the individual or species.

The diagram here given is intended to roughly illustrate

```
        K  L  M              U     C  X         H      I
  ∞     ‿‿‿                                     ‿‿‿‿
        V     W        T     U     C  X            Z
  ∞
  q   vₓ    wₓ         tᵧ    uₓ   c  xₓ              zᵧ
        ·     ·          ·     ·     ·   ·      yₗ      ·
  n   v₁    w₁          ·     ·     ·  x₁    y₁        ·
      ‿‿‿‿‿‿            ·     ·     ·   ·
  m      aₘ             ·     ·        lₘ         ·  eₘ
         ·            t₁    u₁      ·      s     ·  ·
  l      aₗ             kₗ      cₗ     lₗ    ·      ·  eₗ
         ·             ·       ·       ·  s₁   z₁   ·
  k      ·             ·    bₖ  ·       ·     rₖ    ·
         ·             ·       ·       ·        ·
  2   a₂  ·  e₂    f₂  ·  k₂   ·   ·       ·      ·   ·
  1      a₁  ·  ·  ·  k₁   ·   ·       l₁  ·  r₁   ·
          ‿‿‿‿‿‿‿‿‿                    ‿‿‿‿‿
              A            B   C        D        E
```
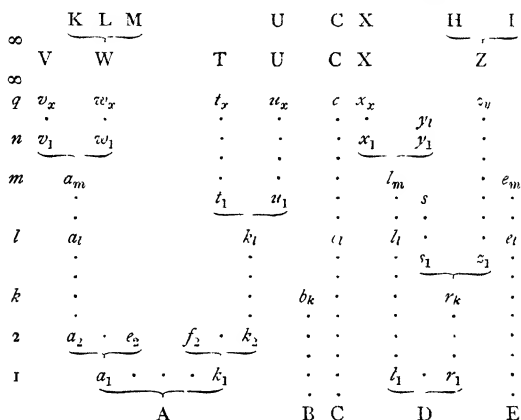
the origin of new forms from pre-existing forms by aid of natural selection or survival of the fittest. Let us suppose that at a certain period of time there are five species, represented by the letters A to E, living in a given region, and let us further suppose that A and D are represented by many, B, C, and E by comparatively few, individuals. Take first the case of A. The offspring of the various individuals will form a large number, represented by the letters $a_1 \ldots k_1$ As we have seen they will vary in their characters. Suppose a_1 to represent those individuals which possess in the most marked degree a certain character (*e.g.* length of flower-tube, as above considered) which in the struggle for existence will be advantageous to them. Suppose k_1 to represent another group possessing in a high degree some other beneficial character; the intermediate groups consist of individuals possessing these characters in a less marked degree. Then,

in the struggle for existence, the tendency will be for the groups a_1 and k_1 to defeat the intermediate groups and *also the parent form*. It will not, probably, happen that the groups a_1 k_1 will be the only survivors, but they will produce the greatest number of offspring. In the next generation the offspring will again vary in the same characters and the tendency will again be to the selection of those that vary furthest in favourable directions, *i.e.* the groups a_2 k_2 will tend to produce most offspring, whilst the intermediate groups, which vary back in the direction of the original form, will tend to die out or produce but few offspring. The same process may be repeated in every successive generation, and thus the original species will give rise to steadily *diverging* lines of offspring (the divergence is not shown in the diagram beyond the second generation). After a large number of generations, the differences between the group a and the group k, at first infinitesimal, will become obvious, and we may now say that the species A has two *varieties*, a and k. The type form A itself will usually have ceased to exist in this locality, but if one of the varieties to which it has given rise be much commoner than the others, naturalists generally term this the 'type' of the species, unless, as often happens, the new variety or varieties have arisen on the margin of the area of the earth's surface occupied by the species. This seems to be very common, and the parent species may continue to exist side by side with the variety for a long time.

Varieties are common in most of the larger genera and species, *e.g.* Rosa, Rubus, Hieracium, Salix. They differ from one another chiefly in small and variable characters, especially of the vegetative organs; *e.g.* there are two varieties of the common buttercup (*Ranunculus acris*), one of which, var. *Steveni* Reich., has the stem slightly hairy at the base and the segments of the radical leaves not over-lapping; while the other, var. *vulgatus* Jord., has the stem densely hairy at the base and the leaf-segments overlapping. The student should work through Hooker's *British Flora* and note the divergences of character usually considered as sufficient to mark varieties. He can hardly fail to be struck by the apparently trivial nature of the differences, and will often be at a loss to understand what value they can possess

in the struggle for existence. This point cannot be discussed here; we can only refer to what has been said above as to the possible value of any variation, and as to correlated variation. The external marks of difference are often, it is possible, merely expressions (perhaps themselves useless) of some constitutional difference indistinguishable by us.

To return to the diagram, we imagine the original species A now represented by the two varieties a_1 and k_1. The latter may now be imagined to diverge again into two new varieties, t and u, and afterwards a into v and w, and at the stage marked by the letter q the species will thus have four varieties. It is obvious that the differences between v and w will be but slight, most of their characters being the same as those of the parent form a; the same may be said of t and u, but they will be rather more widely separated in character. The differences between the two pairs of varieties, on the other hand, will be considerable, as they are separated by so many generations from the common ancestor A.

The divergence of the four varieties continuing, will ultimately reach a point where the differences become so considerable that the forms will have to be ranked as *species*. The forms t and u will reach this condition first. To define exactly what is meant by species is impossible; different naturalists rank the same forms as species or varieties, *e.g.* in the genera Rubus, Hieracium, &c., the innumerable varieties are ranked as species by some authors. Two nearly allied species will have many characters in common derived from the common ancestor, but they will differ more from one another than do varieties, and their characters will be rather more fixed. Varieties when crossed yield fertile offspring, whereas the offspring of two species (*hybrids*) are usually comparatively sterile (cf. the case of heterostyled flowers; see p. 88, and Lythrum &c. in Pt. II.). The student should work at the determination of species until he becomes familiar with the kind of characters that give specific distinction. He will note that they are chiefly characters of the vegetative organs, and minor characters of flowers &c. The diagnosis of species in Hooker's *British Flora* is a mean between the extremes of Bentham and Babington, and the student will do well to follow it, but with frequent reference to, and comparison with, the other two writers.

The original species A has thus, after a considerable lapse of time, given rise to four new species, T, U, V, W, by which it is now represented on the earth's surface. Let us now consider the case of B, a species supposed nearly allied to A and represented by but few individuals. The chance of a favourable variation appearing in a number of the offspring is small; let us suppose that none appears, then B will go on as usual. Presently however the form represented by the divergent line *k* from A trespasses upon B's territory and comes into competition with it. Let us imagine *k* more numerous and better adapted to the general conditions of life than B, then the latter will gradually die out and become extinct. This extinction of old forms, whose numbers gradually dwindle from generation to generation, is a common phenomenon, as geology teaches. During the last few ages of geological history, to the present time, it would seem that the total number of species existing at any one time has remained fairly constant, old ones having died out as new ones have become formed.

Now take the case of C, also a species of few individuals. This we may suppose not to become extinct during the period under consideration, because it has had a favourable situation, little competition, or a very peculiar mode of life, or some other advantage. It therefore appears in the top line, representing the later period. D is supposed to be a species with many individuals, and one therefore in which favourable variations are more likely to arise. It gives rise to four varieties, but ultimately only to two species, X and Z, the latter exterminating the small species E, which had survived for a long period.

The above is a crude outline, but may serve to give a general idea of the theory of evolution by natural selection. Of course more than one character will vary at once, and the actual problem is more complex than the simple case we have dealt with, but if one could split up the factors in the problem each would probably give this sort of result.

Let us now follow the evolution a step further. The four species T, U, V, W are nearly allied. Then after a long period they will again give rise to new species, represented by the letters in the top row. The species K, L, M derived from W will be nearly allied in character, but will differ

much from U and still more from C, from X, and from the two species H and I (derived from Z). The divergence between these various groups will now be so great that they will be regarded as *genera*, one with three species, one with two, and the rest each with one species. The common ancestor of the species of a genus is far back, but the common ancestor of two allied genera farther still. Genera agree in fewer characters than do species. The characters that mark genera should be studied in a flora (see also Coniferae in Pt. II.); it will be noticed that floral characters enter more largely into the diagnoses than in the case of species. The genus represented by the one species C will be what is called an *archaic* genus, a type belonging to a former age. Several examples of this kind may be met with, *e.g.* Casuarina, Isoetes, Phylloglossum, &c.

Just as varieties gradually diverge into species and these into genera, so these again form groups of genera, or *natural orders*. The characters of all the natural orders are given in full in Part II. and should be studied there, especially by the method of comparison of allied orders. The orders may be grouped into *cohorts*, these into *series*, and so on.

It is necessary to keep clearly in mind the fact that the ancestral forms die out as species diverge, and can only be found, if at all, as fossils. The archaic forms of vegetation now existing are of special interest as types of a preexisting flora, but they must not be regarded as representing the ancestral forms from which our existing vegetation of higher types is derived. A consideration of the diagram and explanation above given will show this clearly, but it is necessary to emphasise it here, as this error is a common product of the 'type' system of teaching. The study of fossil botany has brought to light many interesting relics of past vegetation, but probably few, if any, of these are direct ancestors of now existing forms. It must be remembered that those plants which are of woody nature are most likely to be preserved. Now the general upward evolution to the highest flowering plants appears to have taken place in herbaceous plants. Only in these plants does generation succeed generation rapidly, and thus evolution can go on more quickly than in trees or shrubs. Such families as consist entirely of the latter require an enormously longer time to give rise to

new groups than do herbaceous families. Hence we can easily understand why most of our fossils represent forms which have died out and left no posterity. This point is one of importance also in dealing with such orders as the Cycads or Coniferae. These are all trees or shrubs, therefore the common ancestor of each group was very probably a tree or shrub also, and hence would not be a link in the direct upward chain leading to the higher flowering plants.

It will frequently happen that as new forms are evolved from older ones, certain organs will become useless. These will then be disadvantageous in that they cause a waste of material, and perhaps in other ways. Hence they will tend to be eliminated by natural selection, which will pick out on the whole those individuals in which these organs are smallest. Thus in course of time the organ will become *rudimentary*, reduced to a small vestige of its former self. Such are the stamens in female flowers of dioecious or gynodioecious plants, the leaves in Ruscus, &c. The organ will not often, perhaps, disappear altogether, as when reduced to very small dimensions it will be too insignificant to cause any disadvantage to the plant. It will thus remain as a very important testimony to the descent of the plant, indicating the presence in the remote ancestors of an efficient organ in the position occupied by it. Such rudimentary organs are of great importance in classificatory work.

Principles of Classification. What we have said above must suffice as an indication of the general plan of the vegetable kingdom, which may be represented by a tree, the existing species being the tips of the branches, and the older parts of the stems representing forms now extinct. We shall expect, then, to find that plants can be arranged in groups under groups, and this is actually the case. Species are grouped into genera, these into orders, and so on. If our museums of fossils could supply us with all the forms of vegetable life that have existed on the earth classification would be an easy task. As it is, however, we possess only the tips of the twigs, so to speak, and have to fit them into their proper places on the tree. This is done by careful and detailed comparison of all the characters of the various organisms; those which agree in a

large number of characters are considered as nearly related, those which agree in few as more distantly related, to one another. The ideal to be aimed at in classification is a systematic arrangement of all known forms, existing or fossil, to show their mutual relationships, and grouped into genera, orders, &c. It is obvious that an ordinary written scheme of classification can never completely fulfil this object, for it endeavours to represent on a plane surface what can only be accurately shown in the solid.

Plants show, as we have seen, varying degrees of resemblance to one another. The older naturalists recognised this fact, and talked of the *affinities* of organisms, but it was Darwin who first showed that affinity meant relationship. The *natural* system of classification, which tries to group plants according to their affinities, was already well advanced before 1859, and has since been brought nearer to perfection, though there is yet a very great deal of work to be done.

A classification which only takes account of a few characters is found not to show relationships at all truly, such is the famous *artificial* system of Linnæus, a most convenient arrangement for practical use, but now superseded by the natural system. We must always work with the *aggregate* of characters of every species; this is easily understood after what we have said above. Very often, indeed, a single character or combination of characters enables us to recognise the approximate relationship of a species very easily, but its exact relationship can only be determined by a study of all its characters.

In practice, naturalists regard a character as of high importance for classification if it is nearly uniform and common to a large number of species. This is evidently, upon the theory of descent, a character that has been handed down unaltered from very old times and is common to the descendants of a form that existed very far back in the history of plants. It may thus be used as a diagnostic character of a large group; as an example we may quote the instance of the division of Angiosperms into two groups according to whether they have one or two cotyledons in the embryo. Characters of more variable nature and common to fewer species mark smaller groups, and so on.

We may now consider the kind of characters used. "The less any part of the organism is concerned with special habits the more important it is for classification." This is easily understood, for such a part will be much less liable to rapid variation and modification. The vegetative organs, therefore, are comparatively useless in diagnosing the larger groups. There are however vegetative characters which are not so liable to modification and are therefore useful; such are the alternate or opposite arrangement of the leaves, their veining, &c. The embryonic characters of the vegetative organs, *e.g.* the number of cotyledons, are important. Rudimentary organs are often of great importance in classification. The characters of flower and fruit are the most important for diagnosis of large groups. It is necessary to recognise, however, the kind of floral character to use. We have seen (p. 66) the importance of cohesion of parts. Once acquired, it is not likely to be lost and may be handed down to a large number of descendants; the amount of cohesion, on the other hand, is a very variable character. In the same way, the existence or non-existence of adhesion, the shape of the receptacle, irregularity, number of members in a whorl, introrse or extrorse opening of anthers, &c. are all important. The characters of the gynœceum are very useful, *e.g.* the placentation, the position of the raphe of the ovule, the anatropy &c. of the ovules, and so on. The number of cotyledons, the shape of the embryo, and the presence or absence of endosperm in the seed, are also good characters. All these are largely used for the diagnosis of the larger groups, as will be seen by a study of the tables below and of the characters of the orders in Part II. The characters of vegetative organs and the more easily modified floral characters are chiefly used in the diagnosis of genera and species.

A very important point to recognise is this, that a given character may be good in one group of plants, and in another may be nearly useless and exhibit a great deal of variation; this is easily understood on the theory of descent. For example, whether a flower is perigynous, epigynous or hypogynous is usually an important character, used in diagnosing natural orders, but in the genus Saxifraga all

three conditions may be found. Other illustrations are Nigella in Ranunculaceae with its syncarpous gynœceum, Vaccinium in Ericaceae, and so on.

Systems of Classification. It is evident from what has been said above that in any written system of classification there must be a considerable element of artificial grouping of plants. For practical purposes this matters little, and when once a system has been adopted for use it is well to adhere to it; in large herbaria, for example, it is impossible to make frequent changes of arrangement to suit the progress of knowledge. But this is no reason why everyone should be compelled to use an antiquated classification. Each generation of students should be trained in the system which offers the closest approach to the representation of the knowledge of the day. The system of Bentham and Hooker, proposed in their *Genera Plantarum*, has remained the standard one in Britain for a long time, but on the Continent has long been superseded by the more natural system based on that of Brongniart. The latest exposition of this system is that of Engler in the *Syllabus der Vorlesungen*, and in *Die natürlichen Pflanzenfamilien*. We have therefore adopted this system for the flowering plants, but a key is also given to the system of Bentham and Hooker, so that those who prefer may use the latter. The natural orders given in Part II. are those of Engler, but their place in the other systems is always indicated. A third system, outlined below, is that of Eichler, adopted by Warming (*Systematic Botany*, English ed.); it resembles that of Engler very closely. The ferns and their allies are classified according to the most recent views upon the subject.

The Vegetable Kingdom is primarily divided into four groups :

Thallophyta—Algae and Fungi.

Bryophyta—Mosses and Liverworts.

Pteridophyta or Vascular Cryptogams—Ferns, Lycopods, Equisetums, &c.

Spermaphyta or Phanerogams—Seed-plants or so-called flowering plants (see Pt. II.).

With the first two groups we are not concerned in this work. The classification of the Ferns, &c. is given in

Pt. II. (art. Pteridophyta, &c.). We shall deal here with the last and highest group.

The primary division of the Spermaphytes in all systems is into Gymnosperms and Angiosperms, but it is probable that this is very artificial—that the former are really three classes derived from separate stocks of the early Pterido-phyta, and the latter really two or more classes derived possibly from primitive Gymnosperms. The Angiosperms are divided into Mono- and Di-cotyledons in all systems, but the further subdivisions vary. The outline given below gives the characters of these groups as far as the cohorts; the characters of the orders must be sought in Part II.

SYSTEM OF ENGLER, 1892—96.

SPERMAPHYTA.

GYMNOSPERMAE.

(Ovules before pollination not enclosed in an ovary formed of infolded or united carpels; endosperm formed before fertilisation; see G. in Pt. II.)

Class I. Cycadales (stem with little or no branching; leaves pinnately divided, forming a rosette at end of stem; flrs. diœcious, not massed in infl.; no perianth):

N. O. 1. Cycadaceae.

Class II. Coniferae (stem branched; leaves usually narrow, often linear; flrs. unisexual; no perianth):

N. O. 2. Araucariaceae. 3. Taxaceae.

Class III. Gnetales (stem simple or branched; leaves in pairs, undivided; flrs. unisexual or ⚥, with perianth, and more or less enclosed in bracts):

N. O. 4. Gnetaceae.

ANGIOSPERMAE.

(Ovules produced in an ovary formed of coherent carpels or of one carpel with coherent margins; endosperm formed after fertilisation; see A. and Chalazogamae in Pt. II.)

Class I. Monocotyledones (embryo with one cotyledon; stem with closed vascular bundles, 'scattered' as seen in cross-section; leaves usually parallel-veined; flrs. usually 3-merous; see M. in Pt. II.):

Cohort 1. *Pandanales* (flr. naked or with homochlam., bract-like perianth, unisexual; sta. $1—\infty$; cpls. $1—\infty$; endosperm; infl. compound, spherical or cylindrical):

N. O. 5. Typhaceae. 6. Pandanaceae. 7. Sparganiaceae.

Cohort 2. *Helobieae* (flr. cyclic or hemi-cyclic; perianth o or in 1 or 2 whorls, homo- or hetero-chlam., hypogynous or epigynous; sta. 1—∞; cpls. 1—∞, apo- or syn-carpous; endosperm little or none; water or marsh plants or saprophytes):

N. O. 8. Potamogetonaceae. 9. Naiadaceae. 10. Aponogeton-aceae. 11. Juncaginaceae. 12. Alismaceae. 13. Butomaceae. 14. Triuridaceae. 15. Hydrocharitaceae.

Cohort 3. *Glumiflorae* (flr. naked, rarely with hair-like or true perianth, covered by glumes; ovary 1-loc. with 1 ovule):

N. O. 16. Gramineae. 17. Cyperaceae.

Cohort 4. *Principes* (flr. usually cyclic, homochlam., 3-merous, hypogynous, regular or rarely zygomorphic; cpls. 3, usually each with 1 fleshy ovule; stem monopodial with fan-like or pinnate leaves; infl. a simple or compound spadix):

N. O. 18. Palmae.

Cohort 5. *Synanthae* (flr. always unisexual; ♂ naked or with thick shortly-toothed perianth and 6—∞ sta.; ♀ naked or with 4 fleshy scale-like leaves, before each of which is a long thread-like staminode; cpls. (2) or (4), with 2 or 4 placentae, and ∞ ovules, sunk in axis of spadix):

N. O. 19. Cyclanthaceae.

Cohort 6. *Spathiflorae* (flr. cyclic, with o, 1, or 2 whorls of perianth, 3- or 2-merous, ♀ or unisexual, often much reduced, even to 1 sta. or cpl.; spadices simple, enclosed in spathes, with no bracts; sympodial plants, rarely with well-developed stems):

N. O. 20. Araceae. 21. Lemnaceae.

Cohort 7. *Farinosae* (flr. homo- or hetero-chlam., 3- or 2-merous, usually P 3 + 3, A 3 + 3, G (3); one whorl of sta. is sometimes wanting, or all sta. but 1; ovules often orthotropous; endosperm mealy):

N. O. 22. Flagellariaceae. 23. Restionaceae. 24. Centrolepidaceae. 25. Mayacaceae. 26. Xyridaceae. 27. Eriocaulaceae. 28. Rapate-aceae. 29. Bromeliaceae. 30. Commelinaceae. 31. Pontederiaceae. 32. Philydraceae.

Cohort 8. *Liliiflorae* (like 7, but endosperm fleshy or cartilaginous; ovules usually anatropous; flrs. sometimes 4- or 5-merous):

N. O. 33. Juncaceae. 34. Stemonaceae. 35. Liliaceae. 36. Haemodoraceae. 37. Amaryllidaceae. 38. Velloziaceae. 39. Tac-caceae. 40. Dioscoreaceae. 41. Iridaceae.

Cohort 9. *Scitamineae* (flr. cyclic, homo- or hetero-chlam., 3-merous, typically diplostemonous but often with reduction of androeceum even to 1 sta., usually epigynous and zygomorphic; ovary usually 3-loc. with large ovules; seeds usually with arils and with endo- and peri-sperm; tropical plants):

N. O. 42. Musaceae. 43. Zingiberaceae. 44. Cannaceae. 45. Marantaceae.

Cohort 10. *Microspermae* (flr. cyclic, homo- or hetero-chlam., typically diplostemonous but often with important reduction; ovary inferior, 3- or 1-loc. with ∞ small ovules; endosperm or none):

N. O. 46. Burmanniaceae. 47. Orchidaceae.

Class II. Dicotyledones (embryo with two cotyledons; stem with open vascular bundles usually in a single ring; leaf net-veined; flr. usually 5-, 4- or 2-merous; see D. in Pt. II.) :

SERIES I. ARCHICHLAMYDEAE. Perianth in lower stages of development, *i.e.* either (1) absent, (2) simple, in one whorl, petaloid or sepaloid, (3) in two whorls, the inner polyphyllous, (4) in two whorls, the inner gamophyllous (rare; in forms whose nearest relatives are polyphyllous, *e.g* Correa in Rutaceae), or (5) in one whorl, in consequence of the abortion of the inner whorl

Cohort 1. *Piperales* (flr. naked or homochlam , ☿ or unisexual; sta 1—10, cpls. 1—4 free or united; flrs very small, in spikes; leaves undivided, with stipules or none):

N. O. 48. Saururaceae. 49. Piperaceae. 50. Chloranthaceae. 51. Lacistemaceae.

Cohort 2. *Juglandales* (flr. unisexual, naked or with sepaloid perianth; sta. 2—40, cpls. 2 or 1; ovary 1-loc with 1 basal orthotropous or rarely parietal amphitropous ovule, drupe, no stipules):

N.O. 52 Juglandaceae. 53. Myricaceae. 54 Leitneriaceae.

Cohort 3 *Salicales* (flr. naked, dioecious, with cup like disc, some times reduced to tooth-like scales, sta. 2—∞, cpls (2), G̲ 1-loc. with ∞ anatropous ovules on parietal placentae, capsule with ∞ seeds, seed small, exalbuminous, with basal tuft of hairs; woody plants with undivided, rarely lobed, alternate, stipulate leaves and spikes of flrs.):

N.O. 55. Salicaceae

Cohort 4 *Fagales* (flr. cyclic, homochlam., rarely naked, generally unisexual, monœcious; sta often anteposed to perianth-leaves; cpls. (2—6) each with 1—2 ovules, G̲; fruit usually nut-like, 1-seeded; no endosperm; flrs in simple or compound spikes)

N.O 56. Betulaceae 57. Fagaceae.

Order of doubtful position, allied to 56.

N. O. 58. Casuarinaceae (flrs unisexual; ♂ in spikes, with 2 perianth-leaves and 1 sta.; ♀ in heads, naked, of (2) cpls; ovules 2, in anterior loc only, orthotropous, basal; nut enclosed in woody bracteoles; seed exalbuminous)

Cohort 5. *Urticales* (flr cyclic, homochlam , rarely naked, usually 2 merous, rarely 2 + 3, generally regular, sta. anteposed to perianth-leaves; cpls. 2—1; G̲ with 1 ovule, nut, flrs. usually in cymose panicles):

N.O. 59. Ulmaceae 60. Moraceae. 61. Urticaceae.

Cohort 6 *Proteales* (flr cyclic, homochlam., usually 2-merous with sta. anteposed to perianth leaves, hypogynous, ☿ or unisexual, regular or not; perianth petaloid; sta rarely quite free, usually united to perianth all but the anthers; G̲ 1)

N. O. 62. Proteaceae.

Cohort 7. *Santalales* (flr cyclic, homochlam with sta anteposed to perianth-leaves, rarely heterochlam. and haplo or diplo stemonous; G̲ (2—3) rarely 1, each cpl with 1 ovule pendulous from apex of loc. or from free-central placenta; sometimes—in order 63—the ovules and placentae are not differentiated, but the embryo-sacs are in the tissue filling the interior of the ovary):

N.O 63 Loranthaceae. 64 Myzodendraceae. 65. Santalaceae. 66. Grubbiaceae. 67. Olacaceae. 68. Balanophoraceae.

Cohort 8. *Aristolochiales* (flr. cyclic, homochlam., epigynous, regular

or zygomorphic; perianth petaloid; ovary usually inferior, 4—6-loc. with axile, or 1-loc. with parietal, placentae and ∞ ovules) :

N. O. 69. Aristolochiaceae. 70. Rafflesiaceae. 71. Hydnoraceae.

Cohort 9. Polygonales (flr. homo- or hetero-chlam., regular ; G̲ 1-loc. with 1 erect rarely anatropous ovule; leaves usually with ocreate stipules) :

N. O. 72. Polygonaceae.

Cohort 10. Centrospermae (flr. acyclic or cyclic, homo- or heterochlam.; sta. often as many as and opposite to the perianth-leaves, but also ∞—1 ; cpls. 1—∞ usually united ; G̲ rarely multiloc., generally 1-loc. with 1—∞ campylotropous ovules; perisperm ; embryo curved ; mostly herbs) :

N. O. 73. Chenopodiaceae. 74. Amarantaceae. 75. Nyctaginaceae. 76. Cynocrambaceae. 77. Batidaceae. 78. Phytolaccaceae. 79. Aizoaceae. 80. Portulacaceae. 81. Basellaceae. 82. Caryophyllaceae.

Cohort 11. Ranales (flr. spiral to cyclic, regular or not, homo- to hetero-chlam., epi- to hypo-gynous, usually with ∞ sta. ; cpls. ∞—1, usually free, rarely united) :

N. O. 83. Nymphaeaceae. 84. Ceratophyllaceae. 85. Magnoliaceae. 86. Lactoridaceae. 87. Trochodendraceae. 88. Anonaceae. 89. Myristicaceae. 90. Ranunculaceae. 91. Lardizabalaceae. 92. Berberidaceae. 93. Menispermaceae. 94. Calycanthaceae. 95. Monimiaceae. 96. Lauraceae. 97. Hernandiaceae.

Cohort 12. Rhœadales (flr. cyclic, except sometimes the sta., heterochlam., rarely apetalous or homochlam. [order 103], hypogynous, regular or not ; cpls. (∞—2), ovary superior) :

N. O. 98. Papaveraceae. 99. Cruciferae. 100. Tovariaceae. 101. Capparidaceae. 102. Resedaceae. 103. Moringaceae.

Cohort 13. Sarraceniales (flr. hemicyclic to cyclic, homo- or heterochlam., hypogynous, regular ; G̲ (3—5) with parietal or axile placentae and ∞ ovules; seed small, with endosperm ; herbs, usually with alt. entire insect-catching leaves) :

N. O. 104. Sarraceniaceae. 105. Nepenthaceae. 106. Droseraceae.

Cohort 14. Rosales (flr. cyclic, heterochlam. or apetalous, hypo- to epi-gynous, regular or zygomorphic; cpls. free or united ; boundaries of orders badly defined) :

N. O. 107. Podostemaceae. 108. Crassulaceae. 109. Cephalotaceae. 110. Saxifragaceae. 111. Cunoniaceae. 112. Myrothamnaceae. 113. Pittosporaceae. 114. Hamamelidaceae. 115. Bruniaceae. 116. Platanaceae. 117. Rosaceae. 118. Connaraceae. 119. Leguminosae.

Cohort 15. Geraniales (flr. cyclic, heterochlam. or apetalous, rarely naked, usually 5-merous; androeceum various ; cpls. (5—2), rarely more, in 1 whorl, often separated from one another again when ripe, usually with 2—1 rarely ∞ ovules; ovule with ventral raphe and micropyle facing upwards, or, if > 1 ovule present, some sometimes with dorsal raphe and micropyle facing downwards) :

A. Flr. heterochlam., rarely apetalous, usually regular ; sta. generally obdiplostemonous, rarely haplostemonous ; in the zygomorphic flrs. single sta. often aborted ; anthers opening by longitudinal slits; G iso- or oligo-merous ; no secretory cells or cavities.

N. O. 120. Geraniaceae. 121. Oxalidaceae. 122. Tropaeolaceae.

123. Linaceae. 124. Humiriaceae. 125. Erythroxylaceae. 126. Zygophyllaceae.

B. As *A*, but secretory cells, cavities or passages present; in order 129 only sometimes in pith and cortex.

N. O. 127. Cneoraceae. 128. Rutaceae. 129. Simarubaceae. 130. Burseraceae. 131. Meliaceae.

C. As *A*, but flrs., at least in gynœceum, obliquely zygomorphic; leaves often opposite.

N. O. 132. Malpighiaceae. 133. Trigoniaceae. 134. Vochysiaceae.

D. Flr. regular or zygomorphic with 2 whorls of sta.; anthers opening by pores; cpls. (2) median.

N. O. 135. Tremandraceae. 136. Polygalaceae.

E. Flr. regular or zygomorphic with 1 whorl of sta.; petals free or united; seed sometimes with caruncle.

N. O. 137. Chailletiaceae (Dichapetalaceae).

F. Flr. regular, unisexual, often much reduced; cpls. usually (3), each with 2—1 ovules.

N. O. 138. Euphorbiaceae.

G. Order of doubtful position.

N. O. 139. Callitrichaceae.

Cohort 16. *Sapindales* (as 15, but ovules in the reverse position, either pendulous with dorsal raphe and micropyle facing upwards, or ascending with ventral raphe and micropyle facing downwards):

A. Flr. with one whorl of perianth.

N. O. 140. Buxaceae.

B. Flr. heterochlam., regular; gynœceum isomerous or pleomerous.

N. O. 141. Empetraceae. 142. Coriariaceae. 143. Cyrillaceae. 144. Limnanthaceae.

C. Flr. heterochlam., sometimes apetalous, always regular; gynœceum rarely isomerous, tending to oligomery.

N. O. 145. Anacardiaceae. 146. Celastraceae. 147. Aquifoliaceae. 148. Stackhousiaceae. 149. Hippocrateaceae. 150. Icacinaceae. 151. Staphyleaceae.

D. Flr. heterochlam., typically diplostemonous, but with abortion of some sta. or cpls., regular or obliquely zygomorphic.

N. O. 152. Aceraceae. 153. Hippocastanaceae. 154. Sapindaceae.

E. Flr. heterochlam., zygomorphic, haplostemonous.

N. O. 155. Sabiaceae. 156. Melianthaceae. 157. Balsaminaceae.

Cohort 17. *Rhamnales* (flr. cyclic, diplochlam., sometimes apetalous, haplostemonous with sta. opp. to petals, regular; cpls. (5—2) each with 1—2 ascending ovules with ventral raphe):

N. O. 158. Rhamnaceae. 159. Vitaceae.

Cohort 18. *Malvales* (flr. cyclic, heterochlam., rarely apetalous, ☿ or rarely unisexual, usually regular; K and C usually 5-merous; K always valvate; sta. ∞ or in 2 whorls with the inner divided; cpls. (2—∞) each with 1—∞ anatropous ovules):

N. O. 160. Elaeocarpaceae. 161. Tiliaceae. 162. Malvaceae. 163. Bombacaceae. 164. Sterculiaceae.

Cohort 19. *Parietales* (flr. cyclic or hemicyclic with often ∞ sta.

and cpls., heterochlam., rarely apetalous, hypo- to epi-gynous; cpls. ± united, often with parietal placentae):

A. Gynœceum free on convex axis.

N. O. 165. Dilleniaceae. 166. Eucryphiaceae. 167. Ochnaceae. 168. Caryocaraceae. 169. Marcgraviaceae. 170. Quiinaceae. 171. Chlaenaceae. 172. Theaceae. 173. Stachyuraceae. 174. Guttiferae. 175. Dipterocarpaceae. 176. Ancistrocladaceae. 177. Elatinaceae. 178. Tamaricaceae. 179. Frankeniaceae. 180. Cistaceae. 181. Bixaceae. 182. Canellaceae. 183. Koeberliniaceae. 184. Violaceae.

B. Gynœceum free on convex or in tubular axis, rarely united laterally.

N. O. 185. Flacourtiaceae. 186. Turneraceae. 187. Malesherbiaceae. 188. Passifloraceae. 189. Caricaceae.

C. Gynœceum sunk in axis and united with it.

N. O. 190. Loasaceae. 191. Begoniaceae. 192. Datiscaceae.

Cohort 20. *Opuntiales* (flr. hemicyclic, heterochlam., with ∞ spiral K, C, A, on tubular axis, and 4—∞ cpls. forming an inferior ovary):

N. O. 193. Cactaceae.

Cohort 21. *Thymelaeales* (flr. cyclic, haplo- or hetero-chlam., or apetalous, haplo- or diplo-stemonous, regular; axis tubular, at least in ♂ and ♀ flrs.; cpls. (2—4) forming free gynœceum; mostly woody plants, rarely herbs with undivided leaves):

N. O. 194. Geissolomaceae. 195. Penaeaceae. 196. Oliniaceae. 197. Thymelaeaceae. 198. Elaeagnaceae.

Cohort 22. *Myrtiflorae* (flr. cyclic, heterochlam., rarely apetalous, haplo- or diplo-stemonous; axis tubular; G (2—∞), rarely free, usually united to axis; herbs and woody plants with alternate or more often opposite or whorled leaves):

N. O. 199. Lythraceae. 200. Blattiaceae. 201. Punicaceae. 202. Lecythidaceae. 203. Rhizophoraceae. 204. Myrtaceae. 205. Combretaceae. 206. Melastomaceae. 207. Onagraceae. 208. Hydrocaryaceae. 209. Haloragidaceae.

Cohort 23. *Umbelliflorae* (flr. cyclic, heterochlam., usually haplostemonous, epigynous, 5—4-, rarely ∞-merous, usually ♀, regular; cpls. (5—1) or (∞), each with 1 or rarely 2 pendulous anatropous ovule; seed with rich endosperm; flrs. usually in umbels):

N. O. 210. Araliaceae. 211. Umbelliferae. 212. Cornaceae.

SERIES II. SYMPETALAE. Perianth in higher stage of development, always originally in 2 whorls, the inner gamophyllous (in a few cases polyphyllous or absent, though normal in closely related forms).

Cohort 1. *Ericales* (flr. 5—4-merous, obdiplostemonous or the sta. before the petals absent, ♀, usually regular; petals free or united; sta. hypo- or epi-gynous, rarely united to corolla at base; cpls. (2—∞), when isomerous usually opposite to petals; ovary superior to inferior):

N. O. 213. Clethraceae. 214. Pyrolaceae. 215. Lennoaceae. 216. Ericaceae. 217. Epacridaceae. 218. Diapensiaceae.

Cohort 2. *Primulales* (flr. 5- or rarely 4-∞-merous, typically diplostemonous, but usually haplostemonous with sta. opposite to petals and epipetalous, ♀ or unisexual, usually regular; petals rarely free; ovary

superior to inferior, 1-loc. with ∞—1 ovules on basal or free-central placenta) :

N. O. 219. Myrsinaceae. 220. Primulaceae. 221. Plumbaginaceae.

Cohort 3. Ebenales (flr. diplo- or triplo-stemonous, or haplostemonous by abortion, rarely with ∞ sta.; petals united; ovary multi-loc. with axile placentae, and 1 or few ovules in each loc.) :

N. O. 222. Sapotaceae. 223. Ebenaceae. 224. Symplocaceae. 225. Styracaceae.

Cohort 4. Contortae (flr. usually 5-, rarely 2- to 6-merous, usually sympetalous; sta. usually as many as petals, sometimes fewer, rarely hypogynous, usually united at base to corolla; cpls. (2); corolla usually convolute, sometimes valvate; leaves usually opposite, undivided and exstipulate):

N. O. 226. Oleaceae. 227. Salvadoraceae. 228. Loganiaceae. 229. Gentianaceae. 230. Apocynaceae. 231. Asclepiadaceae.

Cohort 5. Tubiflorae (flr. typically with 4 isomerous whorls, or more often with reduction in gynoeceum, or if zygomorphic also in androeceum; sta. epipetalous):

A. Flr. usually regular; cpl. with few or 2 ovules; leaves usually alternate.

N. O. 232. Convolvulaceae. 233. Polemoniaceae. 234. Hydrophyllaceae. 235. Boraginaceae.

B. Flr. usually zygomorphic; cpl. with 2 or rarely 1 ovules; leaves usually opposite or whorled.

N. O. 236. Verbenaceae. 237. Labiatae. 238. Phrymaceae.

C. Flr. regular or more often zygomorphic, typically 5-merous; sta. 5, 4, or 2; cpls. rarely (5), usually (2), with mostly ∞, rarely 2—1 ovules; fruit usually a capsule, sometimes a berry or drupe; capsule loculicidal only just to the base.

N. O. 239. Nolanaceae. 240. Solanaceae. 241. Scrophulariaceae. 242. Lentibulariaceae. 243. Orobanchaceae. 244. Gesneraceae. 245. Columelliaceae. 246. Bignoniaceae. 247. Pedaliaceae. 248. Martyniaceae. 249. Globulariaceae.

D. Like *C*, but capsule loculicidal to very base.

N. O. 250. Acanthaceae.

E. Flr. 5-merous, regular or zygomorphic; cpls. (2), each with 2—4—8 ovules, or (2—∞), each with 1 pendulous ovule with micropyle facing upwards; drupe, with chambered endocarp or 2—∞ stones.

N. O. 251. Myoporaceae.

Cohort 6. Plantaginales (flr. 4-merous, isomerous except in cpls., ⚥ or unisexual, regular; leaves alternate):

N. O. 252. Plantaginaceae.

Cohort 7. Rubiales (flr. typically 5—4-merous with isomerous sta. and cpls., or with latter oligomerous, regular or zygomorphic; Ḡ multi-loc., with ∞—1 anatropous ovules in each loc.) :

N. O. 253. Rubiaceae. 254. Caprifoliaceae. 255. Adoxaceae (?).

Cohort 8. Aggregatae (flr. typically 5-merous with fewer sta. and cpls., zygomorphic or asymmetric; Ḡ with only 1 fertile loc. and 1 pendulous ovule):

N. O. 256. Valerianaceae. 257. Dipsaceae.

Cohort 9. *Campanulatae* (flr. typically 5-merous with usually fewer cpls.; anthers close together, often united; G multiloc. with ∞—1 ovules in the loculi, or 1-loc. with 1 ovule) :

N. O. 258. Cucurbitaceae. 259. Campanulaceae. 260. Goodeniaceae. 261. Candolleaceae. 262. Calyceraceae. 263. Compositae.

SYSTEM OF BENTHAM AND HOOKER, 1862—93.

PHANEROGAMAE.

I. DICOTYLEDONES (as above).

I. Polypetalae (flr. usually with two whorls of perianth, the inner polyphyllous : exceptions as in Engler's system):

SERIES I. THALAMIFLORAE. Sepals usually distinct and separate, free from ovary; petals 1-, 2- to ∞-seriate, hypogynous; sta. hypogynous, rarely inserted on a short or long torus or on a disc; ovary superior.

Cohort 1. *Ranales* (sta. rarely definite; cpls. free or immersed in torus, very rarely united; micropyle usually inferior; embryo minute in fleshy albumen):

N. O. 1. Ranunculaceae. 2. Dilleniaceae. 3. Calycanthaceae. 4. Magnoliaceae. 5. Anonaceae. 6. Menispermaceae. 7. Berberideae. 8. Nymphaeaceae.

Cohort 2. *Parietales* (sta. definite or ∞ ; cpls. united into a 1-loc. ovary with parietal placentae, rarely spuriously 2- or more-loc. by prolongation of placentae):

N. O. 9. Sarraceniaceae. 10. Papaveraceae. 11. Cruciferae. 12. Capparideae. 13. Resedaceae. 14. Cistineae. 15. Violarieae. 16 Canellaceae. 17. Bixineae.

Cohort 3. *Polygalinae* (K and C 5, rarely 4 or 3; sta. as many or twice as many as petals; ovary 2-, rarely 1- or more-loc.; endosperm fleshy, rarely absent; herbs or shrubs with exstip. leaves):

N. O. 18. Pittosporeae. 19. Tremandreae. 20. Polygaleae. 21. Vochysiaceae.

Cohort 4. *Caryophyllinae* (flr. regular; K 2—5, rarely 6 ; petals usually as many; sta. as many or twice as many, rarely more or fewer; ovary 1-loc. or imperfectly 2—5-loc. ; placenta free-central, rarely parietal; embryo usually curved in floury albumen):

N. O. 22. Frankeniaceae. 23. Caryophylleae. 24. Portulaceae. 25. Tamariscineae.

Cohort 5. *Guttiferales* (flr. regular; K and C usually 4—5, imbricate; sta. usually ∞ ; ovary 3—∞-loc., rarely 2-loc. or of 1 cpl. ; placentae on inner angles of loculi):

N. O. 26. Elatineae. 27. Hypericineae. 28. Guttiferae. 29. Ternstroemiaceae. 30. Dipterocarpeae. 31. Chlaenaceae.

Cohort 6. Malvales (flr. rarely irregular; K 5, rarely 2—4, free or united, valvate or imbricate; petals as many or o; sta. usually ∞, monadelphous; ovary 3—∞-loc., rarely of 1 cpl.; ovules in inner angles of loculi):

N.O. 32. Malvaceae. 33. Sterculiaceae. 34. Tiliaceae.

SERIES II. DISCIFLORAE. Sepals distinct or united, free or adnate to ovary; disc usually conspicuous as a ring or cushion, or spread over the base of the calyx-tube, or confluent with the base of the ovary, or broken up into glands; sta. usually definite, inserted upon or at the outer or inner base of the disc; ovary superior.

Cohort 7. Geraniales (flrs. often irregular; disc usually annular, adnate to the sta. or reduced to glands, rarely o; ovary of several cpls., syncarpous or sub-apocarpous; ovules 1—2, rarely ∞, ascending or pendulous; raphe usually ventral):

N.O. 35. Lineae. 36. Humiriaceae. 37. Malpighiaceae. 38. Zygophylleae. 39. Geraniaceae. 40. Rutaceae. 41. Simarubeae. 42. Ochnaceae. 43. Burseraceae. 44. Meliaceae. 45. Chailletiaceae.

Cohort 8. Olacales (flr. regular, ☿ or unisexual; calyx small; disc free, cupular or annular, rarely glandular or o; ovary entire, 1—∞-loc.; ovules 1—3 in each loc., pendulous; raphe dorsal, integuments confluent with the nucellus; endosperm usually copious, fleshy; embryo small; shrubs or trees; leaves alt., simple, exstip.):

N.O. 46. Olacineae. 47. Ilicineae. 48. Cyrilleae.

Cohort 9. Celastrales (flr. regular, ☿; corolla hypo- or peri-gynous; disc tumid, adnate to base of calyx-tube or lining it; sta. = petals or fewer, rarely twice as many, perigynous or inserted outside the disc or on its edge; ovary usually entire; ovules 1—2 in each loc., erect with ventral raphe; leaves simple, except in order 52):

N.O. 49. Celastrineae. 50. Stackhousieae. 51. Rhamneae. 52. Ampelideae.

Cohort 10. Sapindales (flr. often irregular and unisexual; disc tumid, adnate to base of calyx or lining its tube; sta. perigynous or inserted upon the disc or between it and the ovary, usually definite; ovary entire, lobed or apocarpous; ovules 1—2 in each loc. usually ascending with a ventral raphe, or reversed, or pendulous from a basal funicle, rarely ∞ horizontal; seed usually exalbuminous; embryo often curved or crumpled; shrubs or trees, leaves usually compound):

N.O. 53. Sapindaceae. 54. Sabiaceae. 55. Anacardiaceae.
Anomalous orders or rather genera:
N.O. 56. Coriarieae. 57. Moringeae.

SERIES III. CALYCIFLORAE. Sepals united, rarely free, often adnate to ovary; petals 1-seriate, peri- or epi-gynous; disc adnate to base of calyx, rarely tumid or raised into a torus or gynophore; sta. perigynous, usually inserted on or beneath the outer margin of the disc: ovary often inferior.

Cohort 11. Rosales (flr. usually ☿, regular or irregular; cpls. 1 or more, usually quite free in bud, sometimes variously united afterwards with the calyx-tube or enclosed in the swollen top of the peduncle; styles usually distinct):

N.O. 58. Connaraceae. 59. Leguminosae. 60. Rosaceae. 61.

Saxifrageae. 62. Crassulaceae. 63. Droseraceae. 64. Hamamelideae. 65. Bruniaceae. 66. Halorageae.

Cohort 12. *Myrtales* (flr. regular or sub-regular, usually ⚥ ; ovary syncarpous, usually inferior; style undivided, or very rarely styles free; placentae axile or apical, rarely basal; leaves simple, usually quite entire, rarely 3-foliolate in order 68):

N.O. 67. Rhizophoraceae. 68. Combretaceae. 69. Myrtaceae. 70. Melastomaceae. 71. Lythrarieae. 72. Onagrarieae.

Cohort 13. *Passiflorales* (flr. usually regular, ⚥ or unisexual; ovary usually inferior, syncarpous, 1-loc. with parietal placentae, sometimes 3- or more-loc. by the produced placentae; styles free or connate):

N.O. 73. Samydaceae. 74. Loaseae. 75. Turneraceae. 76. Passifloreae. 77. Cucurbitaceae. 78. Begoniaceae. 79. Datisceae.

Cohort 14. *Ficoidales* (flr. regular or sub-regular ; ovary syncarpous, inferior to superior, 1-loc. with parietal, or 2—∞ -loc. with axile or basal placentae ; embryo curved, with endosperm, or cyclical, or oblique with no endosperm) :

N.O. 80. Cacteae. 81. Ficoideae.

Cohort 15. *Umbellales* (flr. regular, usually ⚥ ; sta. usually definite; ovary inferior, 1—2—∞ -loc.; ovules solitary, pendulous in each loc. from its apex; styles free or united at base; seeds with endosperm; embryo usually minute) :

N.O. 82. Umbelliferae. 83. Araliaceae. 84. Cornaceae.

II. Gamopetalae (flr. usually with two whorls of perianth, the inner gamophyllous; exceptions as in Engler's system):

SERIES I. INFERAE. Ovary inferior; sta. usually as many as corolla-lobes.

Cohort 1. *Rubiales* (flr. regular or irregular; sta. epipetalous; ovary 2—∞ -loc., with 1—∞ ovules in each loc.):

N.O. 85. Caprifoliaceae. 86. Rubiaceae.

Cohort 2. *Asterales* (flr. regular or irregular; sta. epipetalous; ovary 1-loc., 1-ovuled, sometimes > 1-loc. but with only 1 ovule):

N.O. 87. Valerianeae. 88. Dipsaceae. 89. Calycereae. 90. Compositae.

Cohort 3. *Campanales* (flr. usually irregular; sta. usually epigynous; ovary 2—6-loc., with usually ∞ ovules in each loc.):

N.O. 91. Stylidieae. 92. Goodenovieae. 93. Campanulaceae.

SERIES II. HETEROMERAE. Ovary usually superior; sta. epipetalous or free from corolla, opposite or alternate to its segments, or twice as many, or ∞ ; cpls. > 2.

Cohort 4. *Ericales* (flr. usually regular and hypogynous; sta. as many or twice as many as petals; ovary 1—∞ -loc. with 1—∞ ovules in each loc. ; seeds minute) :

N.O. 94. Ericaceae. 95. Vaccinieae. 96. Monotropeae. 97. Epacrideae. 98. Diapensiaceae. 99. Lennoaceae.

Cohort 5. *Primulales* (corolla usually regular and hypogynous, sta. usually = and opposite to corolla-lobes; ovary 1-loc. with free-central or basal placenta and 1—∞ ovules):

N.O. 100. Plumbagineae. 101. Primulaceae. 102. Myrsineae.

Cohort 6. *Ebenales* (corolla usually hypogynous; sta. usually more

than corolla-lobes, or if as many, then opposite to them, except in 103, often ∞ ; ovary 2—∞ loc , ovules usually few, trees or shrubs) .

N.O. 103 Sapotaceae   104 Ebenaceae   105 Styraceae

SERIES III BICARPELLATAE Ovary usually superior; sta. as many as or fewer than corolla-lobes, alternate to them, cpls **2**, rarely 1 or 3

Cohort 7 Gentianales (corolla regular, hypogynous, sta epipetalous, leaves generally opposite)

N O   106 Oleaceae   107 Salvadoraceae   108 Apocynaceae 109. Asclepiadaceae   110 Loganiaceae   111 Gentianaceae

Cohort 8 Polemoniales (corolla regular, hypogynous, sta = corolla-lobes, epipetalous, ovary 1—5-loc , leaves generally alternate)

N O   112 Polemoniaceae   113 Hydrophyllaceae   114 Boragi neae. 115 Convolvulaceae   116 Solanaceae

Cohort 9 Personales (flr usually very irregular; corolla hypogynous, often 2 lipped, sta generally fewer than corolla lobes, usually 4, didyna mous, or 2, ovary 1 —2 or rarely 4 loc , ovules usually ∞)

N O   117 Scrophularineae   118 Orobanchaceae   119 Lenti bularieae   120 Columelliaceae   121 Gesneraceae   122 Bignoniaceae 123 Pedalineae   124 Acanthaceae

Cohort 10 Lamiales (corolla usually 2 lipped, hypogynous, rarely regular, sta as in preceding, ovary 2—4 loc , ovules solitary in loc , or rarely > 1 in orders 125 and 127 , fruit a drupe or nutlets)

N O   125 Myoporineae   126 Selagineae   127 Verbenaceae 128 Labiatae

Anomalous Order

N O   129 Plantagineae

III Monochlamydeae or Incompletae (flr usually with one whorl of perianth, commonly sepaloid, or none)

SERIES I CURVEMBRYAE Terrestrial plants with usually ☿ flrs , sta generally = perianth segments, ovule usually solitary, embryo curved in floury endosperm

N O   130 Nyctagineae   131 Illecebraceae   132 Amarantaceae 133. Chenopodiaceae   134 Phytolaccaceae   135 Batideae. 136. Polygonaceae

SERIES II MULTIOVULATAE AQUATICAE Aquatic plants with syncarpous ovary and ∞ ovules

N.O 137 Podostemaceae

SERIES III MULTIOVULATAE TERRESTRES. Terres trial plants with syncarpous ovary and ∞ ovules

N.O 138 Nepenthaceae   139 Cytinaceae   140 Aristolochieae.

SERIES IV MICREMBRYAE Ovary syn or apo-carpous; ovules usually solitary, embryo very small, surrounded by endosperm.

N.O 141. Piperaceae   142 Chloranthaceae   143 Myristiceae. 144 Monimiaceae

SERIES V DAPHNALES Ovary usually of 1 cpl ; ovules solitary or few, perianth perfect, sepaloid, in 1 or 2 whorls, sta peri gynous.

N.O. 145 Laurineae   146. Proteaceae   147. Thymelaeaceae. 148. Penaeaceae. 149. Elaeagnaceae.

SERIES VI. ACHLAMYDOSPOREAE. Ovary 1-loc., 1—3-ovuled; ovules not apparent till after fertilisation; seed with endosperm, but no testa, adnate to receptacle or pericarp.

N.O. 150. Loranthaceae. 151. Santalaceae. 152. Balanophoreae.

SERIES VII. UNISEXUALES. Flrs. unisexual; ovary syncarpous or of 1 cpl.; ovules solitary or 2 per cpl.; endosperm or none; perianth sepaloid or much reduced or absent.

N.O. 153. Euphorbiaceae. 154. Balanopseae. 155. Urticaceae. 156. Platanaceae. 157. Leitnerieae. 158. Juglandeae. 159. Myricaceae. 160. Casuarineae. 161. Cupuliferae.

SERIES VIII. ANOMALOUS ORDERS. Unisexual orders of doubtful or unknown affinities.

N.O. 162. Salicaceae. 163. Lacistemaceae. 164. Empetraceae. 165. Ceratophylleae.

II. Gymnospermae (as in Engler).

N.O. 166. Gnetaceae. 167. Coniferae. 168. Cycadeae.

III. Monocotyledones (as in Engler).

SERIES I. MICROSPERMAE. Inner perianth petaloid; ovary inferior with 3 parietal or rarely axile placentae; seeds minute, exalbuminous.

N.O. 169. Hydrocharideae. 170. Burmanniaceae. 171. Orchideae.

SERIES II. EPIGYNAE. Perianth partly petaloid; ovary usually inferior; endosperm abundant.

N.O. 172. Scitamineae. 173. Bromeliaceae. 174. Haemodoraceae. 175. Irideae. 176. Amaryllideae. 177. Taccaceae. 178. Dioscoreaceae.

SERIES III. CORONARIEAE. Inner perianth petaloid; ovary usually free, superior; endosperm abundant.

N.O. 179. Roxburghiaceae. 180. Liliaceae. 181. Pontederiaceae. 182. Philydraceae. 183. Xyrideae. 184. Mayacaceae. 185. Commelinaceae. 186. Rapateaceae.

SERIES IV. CALYCINAE. Perianth sepaloid, herbaceous or membranous; ovary &c. as in III.

N.O. 187. Flagellarieae. 188. Juncaceae. 189. Palmae.

SERIES V. NUDIFLORAE. Perianth none, or represented by hairs or scales; cpl. 1 or several syncarpous; ovary superior; ovules 1—∞; endosperm usually present.

N.O. 190. Pandaneae. 191. Cyclanthaceae. 192. Typhaceae. 193. Aroideae. 194. Lemnaceae.

SERIES VI. APOCARPAE. Perianth in 1 or 2 whorls, or none; ovary superior, apocarpous; no endosperm.

N.O. 195. Triurideae. 196. Alismaceae. 197. Naiadaceae.

SERIES VII. GLUMACEAE. Flrs. solitary, sessile in the axils of bracts and arranged in heads or spikelets with bracts; perianth of scales, or none; ovary usually 1-loc., 1-ovuled; endosperm.

N.O. 198. Eriocauleae. 199. Centrolepideae. 200. Restiaceae. 201. Cyperaceae. 202. Gramineae.

SYSTEM OF EICHLER (AND WARMING).

GYMNOSPERMAE (as in Engler).

ANGIOSPERMAE.

I. Monocotyledones.

Cohort 1.　*Helobieae* = coh. 2 of Engler.
　　　　2.　*Glumiflorae* = coh. 3 + order 33.
　　　　3.　*Spadiciflorae* = coh. 1, 4, 5 and 6.
　　　　4.　*Enantioblastae* = orders 23—27 and 30.
　　　　5.　*Liliiflorae* = coh. 8 and orders 22, 28, 29, 31, 32.
　　　　6.　*Scitamineae* = coh. 9.
　　　　7.　*Gynandrae* = coh. 10.

II. Dicotyledones.

SERIES I. *CHORIPETALAE* (= Archichlamydeae).

Cohort 1.　*Saliciflorae* = coh. 3 of Engler.
　　　　2.　*Querciflorae* = coh. 4.
　　　　3.　*Juglandiflorae* = coh. 2.
　　　　4.　*Urticiflorae* = coh. 5 + order 58.
　　　　5.　*Polygoniflorae* = coh. 1 and 9.
　　　　6.　*Curvembryae* = coh. 10.
　　　　7.　*Cactiflorae* = coh. 20.
　　　　8.　*Polycarpicae* = coh. 11.
　　　　9.　*Rhœadinae* = coh. 12 (part).
　　　10.　*Cistiflorae* = coh. 13 and parts of 12 and 19.
　　　11.　*Gruinales* = parts of coh. 15 and 16.
　　　12.　*Columniferae* = coh. 18.
　　　13.　*Tricoccae* = parts of coh. 15 and 16.
　　　14.　*Terebinthinae* = parts of coh. 15 and 16.
　　　15.　*Aesculinae* = parts of coh. 15 and 16.
　　　16.　*Frangulinae* = coh. 17 and part of 16.
　　　17.　*Thymelaeinae* = coh. 21 and 6.
　　　18.　*Saxifraginae* = coh. 14 (except orders 117, 119).
　　　19.　*Rosiflorae* = order 117.
　　　20.　*Leguminosae* = order 119.
　　　21.　*Passiflorinae* = part of coh. 19 and order 258.
　　　22.　*Myrtiflorae* = coh. 22.
　　　23.　*Umbelliflorae* = coh. 23.
　　　24.　*Hysterophyta* = coh. 7 and 8.

SERIES II. *SYMPETALAE.*

Cohort 1.　*Bicornes* = coh. 1 of Engler.
　　　　2.　*Diospyrinae* = coh. 3.
　　　　3.　*Primulinae* = coh. 2.
　　　　4.　*Tubiflorae* = orders 232—234.
　　　　5.　*Personatae* = part of coh. 5 and coh. 6.
　　　　6.　*Nuculiferae* = part of coh. 5.
　　　　7.　*Contortae* = coh. 4.

Cohort 8. *Rubiales*=coh. 7 and order 256.
9. *Campanulinae*=part of coh. 9.
10. *Aggregatae*=orders 257, 262 and 263.

It will be noticed that the two German systems agree in making only two chief groups of Dicotyledons; the English system, on the other hand, makes a third group, the Incompletae, which is decidedly artificial, separating for instance Chenopodiaceae, &c. far from the Caryophyllaceae to which they are closely allied. In general, the composition of the smaller groups of orders is much the same in all systems; the differences lie chiefly in the composition and arrangement of the larger groups, as is easily understood from what we have said above. The elementary student should not concern himself with any system of classification until he is well acquainted with a number of orders (see p. 4): he should then carefully study the systems above given and endeavour to discover why their authors have placed such and such orders in the places assigned to them in the various systems. In this way he will gain an insight into the principles of classification. The relationships of many of the orders are discussed in Pt. II. When the student is familiar with 40 or 50 orders, occupying different places in the system he adopts, he will be able to classify approximately any new order that may be presented to him, by determining its affinities to those he already knows. It must be clearly understood that the attempt to use the system to determine the order to which a plant belongs will only lead to difficulties unless the student is already familiar with typical orders from many parts of the system. In actual systematic practice, little if any use is made of the larger groupings, and the position of a plant in the system is recognised by its affinities to others whose positions are known.

Identification of Natural Orders at sight. After a time, the student will find himself becoming able in many cases to recognise at a glance the natural order to which a plant belongs, and after a few years' practice, he should be able in this way to classify most of the plants met with in the field or in a botanic garden. Sometimes the order can be recognised from its general habit, or from belonging to a limited group, *e.g.* water-plants or parasites, in other cases it can be identified with certainty only when in flower.

Thus the Ferns, Equisetaceae, Selaginellas, Cycads, Conifers, Palms, most Araceae, Pandanaceae, Bromeliaceae, Musaceae, Sarraceniaceae, Droseraceae, Cactaceae, Lentibulariaceae, &c. are recognisable by their general habit; Cannaceae, Marantaceae, Zingiberaceae, most Polygonaceae, many Rutaceae and allied orders, Melastomaceae, &c. by their habit taken together with some peculiarity of the vegetative organs; the inflorescence enables one to recognise Typhaceae, Piperaceae, Salicaceae, Betulaceae, Fagaceae, Umbelliferae and their allies, Boraginaceae and allied orders, Dipsaceae and Compositae; obvious floral characters point out such families as Gramineae, Cyperaceae, Liliaceae, Orchidaceae, Proteaceae, Ranunculaceae, Cruciferae, Leguminosae, most Rosaceae, Polygalaceae, Malvaceae and their allies, Melastomaceae, Umbelliferae, Ericaceae, Primulaceae, Asclepiadaceae, Boraginaceae, Labiatae, Rubiaceae, Compositae, &c. When a plant belongs to one of the biological groups described in Ch. III., its identification is often rendered easy by the small number of plants with which comparison has to be made.

Advanced students should consult such works as Darwin's *Origin of Species, Descent of Man, Variation under Domestication;* Wallace's *Darwinism;* Galton's *Natural Inheritance;* Bateson's *Variation;* papers by De Vries in *Ber. D. Bot. Ges.* 1893 onwards, Verschaffelt in the same journal 1894 &c., Ludwig in *Bot. Centr.* 64, 1895, Burkill in *Linn. Soc. Journ.* XXXI 1895; further references will be found in these works. Reference may also be made to the works of H. Spencer, Weismann, Romanes, &c.

CHAPTER III.

Forms of Vegetation, Geographical Distribution of
Plants, &c.

We have dealt above with the general morphology of
both vegetative and reproductive organs and we have seen
that in the higher plants at any rate, the latter are not
subject to much modification in accordance with change of
climate, soil, &c., but rather in accordance with the neces-
sities of the pollination processes. The vegetative organs
on the other hand are intimately related in their structural
and other features to the conditions of climate and soil
under which they exist, and in comparing plants from
different regions we often find great dissimilarity of the
vegetative together with great similarity of the reproductive
systems. It is with this side of the subject that we have
now to deal, considering the vegetation of different regions
both from the morphological and physiological points of
view; we shall thus endeavour to gain an insight at the
same time into the subjects of morphology, natural history,
and geographical distribution of plants. Thus the various
forms of stems usually described together in morphological
works as modified stems will be found treated here, but
their structure is dealt with in connection with their func-
tions, so as to emphasise the important fact that modifica-
tion of the former accompanies modification of the latter.

Adaptation. It is evident, having regard to the
general theory of evolution above sketched, that every
existing species must be fairly well suited to its surround-
ings, but not necessarily perfectly so; if it be very well

suited to existence amid such environment, it will probably increase in numbers, if not, it will probably decrease, and perhaps ultimately become extinct.

The characters of a species are partly inherited and partly *adaptive.* Most of its characters are, as we have seen, derived from some pre-existing species, but a certain number of them will have been acquired in the evolution that has occurred. These will in general be, as has been pointed out above, characters suiting it more closely to the circumstances under which its life is carried on. Such characters, if hereditary and of direct use to the species in its life-history, may be called adaptive characters, or *adaptations* to the mode of life. As time goes on, if the descendants of the species continue to live in similar environments, the adaptive characters will become more and more pronounced, and the inherited characters less so. Of the latter, those which can be usefully modified will often be so modified, those which are useless and do not vary in useful directions will become rudimentary.

It is very difficult to decide in a given case which if any of the characters of a given species are adaptations to its mode of life. A species may possess some character admirably suiting it for one mode of life, though acquired for some other, and if it be found living in the former mode we shall be liable to mistake this character for an adaptation to that mode of life. Examples of this are given below, under Epiphytism. Or again, a species may possess some character of little or no importance in its mode of life but which may prove of great importance in some other environment, should the species happen to be placed there.

The study of adaptation is carried on by the comparison of all forms living in similar surroundings, *e.g.* all water-plants, or all parasites, &c. The members of these biological groups of plants belong usually to many distinct natural orders and their retained ancestral characters therefore differ; if now we find among such a group certain characters in common, which are hereditary and are useful in the particular mode of life characteristic of the group, we may feel pretty sure that we are dealing with genuine adaptations. In such comparative study too, it is brought out in a very striking manner that the same end is attained

in a great variety of ways, *e g* different organs in different species may be modified in their descendants in such a way as to resemble one another in structure and function Good examples of this may be found among xerophytes, *e g* by comparing the various ways in which storage of water, or reduction of the transpiring surface, is effected.

Geographical Distribution of Plants. Under this heading there fall to be considered a number of problems connected with the distribution of plants over the surface of the earth   Why, for example, does the flora of a given country consist of certain species and no others? Why is the flora of Europe different from that of similar areas in North America or elsewhere? Why is any given species, genus, or family confined to a certain area and not found elsewhere, though the conditions of life be favourable? Why is the area occupied by a species (or genus or family) usually continuous, but frequently disjointed or broken up into separate areas? Why are there so many species or genera which occur solely in one spot, usually one island or one mountain chain (such a species or genus is termed *endemic*) and why are such areas characterised by the possession of endemic forms? Why do certain species occur only on the various mountain ranges (*e g* on the Alps, Pyrenees, Carpathians, &c) and not in the intervening lowlands? Why are some species common to Europe and New Zealand? Such questions and many others require solution, and it is the province of botanical geography to deal with them   Space will not permit of more than a brief outline of the subject, sufficient to render intelligible the references to it in Part II and elsewhere, and to add interest to the study of plants in the field or in a botanic garden (see Literature at end of chapter)

We have seen that a species probably arises as a numerous variety in a certain region of the earth's surface and gradually spreads from this point by aid of the seed dispersal methods and by vegetative reproduction (pp 109 and 114).   We can see this process of spreading actually going on in the case of species which have been introduced by man into countries where they were unknown before, *e.g.* species of Lespedeza and Salsola in North America, Gomphocarpus and Mimosa in the tropics, Galinsoga,

Elodea, &c. in Europe, and numerous others. The rapid spreading of many of these in a few years shows that in long periods, such as our science has to deal with, a species even with a very inferior seed-dispersal method might if nothing interfered with it spread over a great part of the globe. Other causes than this must therefore be the checks which have prevented this result. A species at its most flourishing period occupies a definite area, in the midst of which it is commoner than near the margin, and then it is gradually superseded by other forms, and slowly dwindles in numbers and in the extent of area occupied. The causes which limit the area occupied by a species are many, and we shall now briefly deal with them. They may be divided into various heads, *viz.* the *geographical* agents, those which vary with locality, *e.g.* light, heat and moisture, the *topographical* agents, *e.g.* mountains, rivers, seas, the constitution of the soil, &c., the *biological* agents, *e.g.* the distribution of insects and other animals, the mutual competition of organisms, the dependence of one organism upon another, and so on. Last but not least, account has to be taken of the conclusions of geology with regard to alterations in the configuration and climate of the earth's surface, for most of our existing species are descended from forms that existed under different environments.

Light. This agent varies much in different latitudes. Whilst in the tropics the day is always about 12 hours in length and the light nearly vertical at midday, in the arctic regions there is darkness for long periods in winter and almost continuous light in summer, this light moreover coming from almost every side in turn as the sun describes its daily course. Upon the amount and intensity of the light largely depends the amount of assimilation performed, hence the importance of this factor. Plants of high latitudes go through their vegetative period much more rapidly than those of low; thus barley ripens sooner after germination in the far north than it does farther south—the long-continued light favours assimilation. Many plants require brilliant light for full success, others prefer weak light or shade; this difference also comes out in their morphological or anatomical characters, *e.g.* in the *sun-plants* the stems are often short (light retards growth), the leaves often

turned edgewise, the palisade-tissue more developed. Light directly retards growth, and to this fact are due some of the peculiar features of arctic and alpine plants.

Heat. This also depends largely on the latitude, but shows more local variation than light. We have seen (p. 41) how plant functions depend on temperature, and thus the range of temperature in a locality becomes an important factor in determining the species of plants inhabiting it, for some can stand high, some low, temperatures best; others again prefer uniformity of temperature rather than great range. Plants which contain much water are less able to stand extreme cold than those which contain little. High temperatures increase transpiration, and plants with insufficient protection against this will only be able to live in hot countries where there is plenty of moisture.

Atmospheric Moisture, Rain, Snow, &c. Of the three geographical agents in determining distribution, this is perhaps the chief, water being of such very great importance in plant-life. The effects of variation in the degree of saturation of the air are chiefly visible in the transpiration (p. 26); plants transpire more the drier the air is. At the same time, a plant must also regulate its transpiration according to the amount of water available for absorption by the roots; this however is in general proportional to the dampness of the air. Hence we find among plants extreme variety in the rates of transpiration; those living in very dry climates must reduce it to correspond with the available water-supply (see below, Xerophytes, Shore-plants, Epiphytes, &c.).

If the temperature of the air sink sufficiently, precipitation of some of the vapour occurs, as clouds (mist, fog), rain, hail, snow, dew, &c. Upon the form and amount of this precipitation the flora of a region largely depends. Plants living where there is long-continued mist, *e.g.* many alpines, must be able to do without direct sunlight, and to stand a saturated atmosphere. Of the effect of the amount of rain on transpiration we have spoken above, but there are other adaptations to rainfall in existence. Wiesner (*Sitzb. k. Akad. Wien,* 1893, 1894) divides plants into *ombrophiles,* which can undergo without injury long-continued rain, and *ombrophobes,* whose leaves soon decay or fall off

under such circumstances; the plants of the tropics belong mostly to the former, those of deserts to the latter, group. It is of importance to a leaf, for the proper performance of its functions, to keep its surface dry, and in regions of much rain, adaptations for this purpose occur. Of these the most frequent is the *drip-tip* (Träufelspitze) or acuminate leaf-apex (p. 28); the tip of the leaf runs out into a long fine point from which water rapidly drips off. This organ only occurs on leaves whose surfaces are easily wetted by water; many leaves of wet climates have polished surfaces from which water at once runs off, *e.g. Ficus elastica.* The most remarkable drip-tip is that of *Ficus religiosa*; other examples are species of Acer, Artocarpus, Begonia, Boehmeria, Theobroma, &c. (see Pt. II., and Stahl and Jungner in Literature at end of chapter). Many tropical fruits exhibit similar apices, *e.g.* Kigelia, Mucuna. These leaves are generally pendulous with the point downwards, and have usually entire margins; they form the class of leaves termed by Jungner *rain-leaves.* He proposes a second class of *dew-leaves,* occurring chiefly at the boundaries of deserts and steppes; they slope upwards so that water flows from them towards the stem, are obovate, tapering gradually towards the base, and are sessile or shortly stalked. A third class is the *snow-leaves,* found chiefly in regions of normal rainfall and winter snow; they are thin or leathery, serrated, folded in the bud, often rounded, and usually with no pulvinus (see Alpine plants, below).

Wind. Wind tends to increase transpiration and thus in very windy places plants occur with a certain amount of extra protection against evaporation. At the same time the wind dries the soil and thus tends to check absorption of water by the roots.

All these agents are more or less markedly *periodic* in their action, and we find in nearly all plants a *periodicity* in the life history corresponding to that of the geographical agents. In temperate climates this is chiefly determined by the temperature, vegetative activity ceasing in autumn to be resumed in spring. In sub-tropical climates (*e.g.* that of the Mediterranean coasts, &c.) the interruption of vegetative activity occurs in the summer when the heat is great and the drought extreme. Even in tropical climates proper,

with comparatively uniform weather, most plants show a periodicity in the formation of new leaves, flowers, &c. The study of the periodic phenomena of vegetation—dates of flowering, fruiting, &c.—is termed *phaenology.* The periodicity is not merely annual but also daily, as instanced by the phenomena of growth, &c. Removal of a plant to a region of different climate does not at once destroy the periodicity, which is hereditary and ingrained; this is illustrated by the way in which plants from the southern hemisphere continue to flower in our conservatories during the winter months of our year, corresponding to the southern summer. At the same time the periodicity is not as a rule unalterable, and, *acclimatisation* of plants, or alteration of their periodicity to suit other climates, is largely practised, and with success in many cases, especially if the change be not too marked.

Physical Barriers. Of the topographical agents in determining the distribution of species, the natural physical barriers are very important, *e.g.* seas, oceans, deserts, mountain-chains, &c. At the same time, we have seen above (p. 109) that many plants are able to pass over wide expanses of water or over ranges of mountains; these however are but few in proportion to the whole flora, and we generally find the floras on opposite sides of a great natural barrier almost completely different. Ranges of mountains also act as pathways of migration by reason of the new soil frequently exposed in landslips or otherwise; these are seized upon first by plants with good dispersal mechanisms, and thus certain species may travel along the whole range and get into new countries.

Soil. That the nature of the soil has a great influence in determining the flora growing upon it is obvious, but the nature of this influence is still much discussed. It is commonly accepted that it is the chemical rather than the physical composition of the soil that produces most effect. Thus we have a group of plants which grow by preference on soils with much silica (sand), another on chalky soils, and a third on salt soil (halophytes, see below). The amount of water the soil is able to retain is a factor of much importance; so also is the proportion of humus, for if there be very much of it only true saprophytes (see below) or plants

with mycorhiza are able to do well on it. The depth of the soil and its conductivity to heat, and many other factors, also take part in the problem.

Biological Agents. To this group belong those causes of limitation of specific areas which depend upon the interaction of living organisms with one another. Parasites can only spread with their hosts, saprophytes only where there is plenty of suitable humus, *i.e.* usually only where there are woods of certain kinds of trees ; climbers with a few exceptions can only go where there are erect plants or other supports; many plants depend upon insects to a greater or less extent, and the distribution of the latter affects that of the plants (see p. 103), and so on.

Areas occupied by Species, Genera, &c. A species having arisen upon any area of land will tend to spread over that area, but whether it ultimately covers it all or not will depend upon the various agents enumerated above. Many species have an enormous range, *e.g.* from Britain to Kamtschatka, others only a restricted one. A species becomes rarer and rarer towards the limit of its area, if this be determined by general climatic conditions, but may be as numerous at the limit as within the area if the limit be a natural barrier. As it spreads over a large area a species will often give rise to new varieties or even to new species, and thus a genus will be formed, occupying a larger area than any one of its species, but nevertheless a continuous area. The same reasoning applies to a group of genera, natural orders, &c. How then does it come about that so many species, genera, and orders occupy disjointed areas at the present time? As instances may be mentioned the Canellaceae, Hamamelidaceae, Styracaceae, Angelica, Bystropogon, Cedronella, Cedrus, Chiogenes, Desmanthus, Epigaea, Eriocaulon, Neotinea, Pachysandra, Shortia, &c. (see Part II.). Again, how does it happen that many species are common to the various ranges of mountains in each temperate zone, yet do not occur in the intervening lowlands, and how is it that certain forms occur in temperate regions of both Europe and North America, though the bulk of the flora is so unlike in the two cases, and there is no possibility of an 'accidental' transport over such a distance? Accidental transport may account for a few cases in which

the species-area is not very much disjointed, but will not explain the occurrence of many Japanese genera in atlantic America, or other such cases. As a species or family passes its zenith and begins to dwindle, the area occupied by it will be quite likely to become broken into separate portions, but this too is not an explanation of many of the cases quoted. The results of geological science must be summoned to our aid. By their help many of the problems can be solved, and botanical geography can in its turn render useful assistance to the geologist, by pointing out former connecting lines, along which species were formerly continuous or were at least able to migrate. Subsidence may break a continent up into islands, and thus a species that formerly occupied the large area may become disconnected and form the starting point of new species, which taken together form a genus. Or again, elevation may unite islands to continents and cause a mingling of floras, or may form mountain-ranges, which act as barriers. Smaller geological changes than these are sufficient to cause changes of the climate, and thus of the flora, of a region.

The higher plants now existing appear to have developed in comparatively recent times—during the Tertiary period of the earth's history. At first the climate seems to have been warm, and subtropical forms extended even into the polar regions. Gradually the climate grew colder, and species suited to these conditions appeared in the north and gradually followed the tropical plants southwards, ultimately giving rise to our present temperate flora ; as the cold increased, actual arctic species appeared. In the far north the land is continuous or nearly so right round the globe, and many arctic species are circumpolar in distribution at the present day. The similarity of the floras of temperate Europe and North America above-mentioned is usually ascribed to the earlier period when these plants were circumpolar ; they were then gradually driven south and gave rise there to new forms. Later in the tertiary period came the Glacial Era ; the cold spread southwards, driving the tropical plants mostly into the southern hemisphere ; in what is now the northern torrid zone a mixture of temperate and tropical floras probably occurred, whilst arctic species came southwards over America and Europe to the latitude

of the Pyrenees. Afterwards, as the cold retreated, these various northern plants were driven back again by the advance of the southern vegetation, but besides going northwards they would also go up the mountains as new and suitable territory became available at higher and higher levels. This explains how so many northern forms occur on the mountains of the Tropics, and so many arctic genera on those of Europe, and also why there are so many species identical on the different European and even American mountain-ranges, these being in fact species derived from the arctic region in the glacial period. If now we suppose that a glacial period in the southern hemisphere followed that in the northern, those northern plants which had reached the tropical mountains would descend to the plains, mingle with the southern vegetation and go back with it on the return of the warmth, and thus we can explain the appearance of European genera in New Zealand, &c. This sketch will perhaps serve to show the importance of a study of geology in dealing with questions of distribution.

Island-Floras. The flora of such an island as Great Britain, close to and recently detached from a continent, is much like that of the continent, but in true oceanic islands, such as the Sandwich Islands, the Canaries, the Azores, St. Helena, &c., the flora is peculiar, containing a considerable proportion of endemic forms; a study of these floras has led to many important conclusions upon migration, distribution, &c. The endemic forms are sometimes of specific rank only, in which case it seems probable that the isolation of the island cannot have lasted very long, or that it cannot have been long inhabited by plants; sometimes they are of generic rank (*e.g.* see Bencomia, Brexia, Commidendron, Lodoicea, &c.), and in some cases (*e.g. Lactoris fernandeziana* from Juan Fernandez) even of ordinal rank. They illustrate the important conclusion that geographical isolation involves the production of new forms. The most striking examples of this are seen in such archipelagos as the Galapagos Islands, where almost every island has its own endemic species.

The flora of an island may be derived from many sources; islands detached from continents begin with a flora like that of the continent, whilst islands formed by

volcanic agencies or coral-animals begin with no flora and become gradually occupied by plants with dispersal-methods capable of transporting their seeds to it. Thus in the island of Krakatoa Treub (*Ann. Buitenz.* VII.) observed that the ferns were first to arrive, and then coast-plants and those distributed by birds. Besides the more modern forms, such islands as the Azores possess many plants whose presence probably dates from far back in Tertiary times; these have been able to survive on the islands with little or no modification, whilst they have disappeared from the continental areas. The number of species in island-floras is usually very small and the struggle for existence among them probably less keen, and thus not merely have old forms been enabled to survive but the adaptation of the various plants to their environment is not very perfect. This is clearly shown by the way in which introduced species from large continental areas spread over islands at the expense of the indigenous flora. A very large number of European plants are naturalised in most oceanic islands, and many of the native forms have become rare or extinct, *e.g.* in St. Helena and even in such large islands as Australia and New Zealand.

Mountain-Floras. Mountain regions may be compared in many respects with islands, the higher parts differing so much in climate &c. from the lower parts and the lowlands from which they rise as to form isolated regions in which new forms may be evolved. With few exceptions all the higher mountain ranges are characterised by the possession of numerous endemic species and genera. The mountains of Britain, Scandinavia, Kamtschatka, &c. do not show this character. Their flora resembles that of the arctic regions, having been derived from it during the glacial period. In the Pyrenees, Alps, &c., though there are many arctic forms, there are many endemic genera and species.

We have already pointed out that mountain chains act as highways of migration (as do railway-embankments on a small scale). The universally American character of the floras of the different parts of America from north to south is probably in part to be ascribed to the long chain of the Rocky Mountains and the Andes, which has formed a

highway for migration. The general characters of Alpine plants are dealt with below.

Forms of Vegetation. We shall now deal briefly with the morphology and natural history of a number of important *forms of vegetation.* By this term we understand groups of plants, belonging to various natural orders, but presenting a general resemblance in their external habit, often correlated with resemblance in the conditions of life. We shall deal first with the most obvious of these forms, trees, shrubs and herbs, then with such subjects as xerophytes, alpine plants, &c.

Herbs. According to their general habit plants may be roughly divided into *trees, shrubs,* and *herbs;* by the last term are understood plants which do not possess any woody stem above ground, but are made up of softer tissues, and which usually die down to the soil in autumn or after flowering. It is difficult to draw the line between herbs and shrubs; such plants as the wallflower, the base of whose stem is woody and persistent, may be termed *suffruticose* herbs. Many herbs are of great size, *e.g.* the agave, the banana (Musa), Amorphophallus, &c. All the Thallo- and Bryo-phyta are herbaceous, and most existing Pteridophyta, though many fossil trees are known. In the Angiosperms the majority of species are herbaceous, and especially those of the higher orders (p. 129). Herbs are most common in the temperate zones; the damp heat of the tropics is more favourable to the growth of trees.

Herbs may be *annual, biennial* or *perennial;* in the first case the entire life-history from germination to the ripening of the seed is carried out in one year. Some of these plants, *e.g. Stellaria media,* go through several generations in one year, and may be termed *ephemeral.* In an annual plant there is no need for any storage of reserves except in the seeds; the materials formed in the leaves are used directly in growth, flower-formation, &c. Correlated with this is the fact that the flowers are not as a rule very large or conspicuous (such flowers require a lot of material for their formation); most annuals are proletarians (p. 83). It is absolutely essential to the continuance of the race that plenty of seed should be set, and as a rule the flowers do not possess such mechanisms as risk in any degree the

fulfilment of this end; most of them are capable of self-fertilisation, and many are rarely if ever crossed. Vegetative reproduction is rare.

In biennials, *e.g.* the carrot (Daucus), turnip, cabbage, kohl-rabi (Brassica), beetroot (Beta), parsnip (Peucedanum), &c., the case is different, and much storage of reserves takes place. During the first year the plant does not as a rule produce a tall stem or an inflorescence, but usually a rosette of large radical leaves. The food-materials produced in these are much in excess of the immediate requirements of the plant and the balance is stored up in the root (or stem, as in kohl-rabi, or leaves as in cabbage), which becomes thick and fleshy. At the end of the season the leaves usually die down and the plant remains quiescent (*hibernates*) during the winter. Next spring a tall stem is produced, consisting chiefly of an inflorescence, and when the seeds are ripe the plant dies. Practically all the food required during the second year is derived from the reserve-stores, which become completely exhausted. An exaggeration of this feature of biennial plants—the storage of reserves to be used in a single flowering—leads to the peculiar case of the so-called century plant (Agave, q.v.) which saves up materials for many years and uses them all in one great burst of flowers at the end.

In perennial herbs, which live for several or many years, and usually flower each year, the vegetative period is generally interrupted at regular intervals, either by winter, or by the dry season in hot countries; the plant then as a rule dies down. Hence it is necessary that there should be a storage of reserves, to enable the plant to recommence its growth upon the return of spring (or the rainy season). This storage is usually made below ground, where it is well protected, and may be in the root, stem, or leaves. The part in which storage is made is more or less swollen, and if it include a bud is nearly always made to subserve the process of vegetative reproduction (p. 114). In very many cases the original plant does not re-appear in the second season, but in its place appear a number of new plants formed from it by vegetative methods. We shall deal with these cases first.

In many Liliaceae, *e.g.* onion or lily, and other plants,

there is found the peculiar modified shoot termed a *bulb*. It consists of a small disc-like stem at the base, bearing a more or less spherical mass of leaves above, these being closely folded over one another and swollen with reserves ; the leaves in an onion or hyacinth completely enwrap the bulb, which is said to be *tunicated*, whereas in the lily they merely overlap one another and the bulb is said to be *scaly*. The outermost leaves of a tunicated bulb are usually thin, dry, and membranous, protecting the more delicate fleshy leaves. In the centre of the bulb the discoid stem is prolonged into the short inflorescence-axis. Roots are developed adventitiously from the lower side of the stem. It is evident that a bulb is nothing but a large bud with fleshy leaves. When it sprouts in spring or in the rainy season it produces an inflorescence and some green leaves (borne on the same axis as the flowers, or springing from the tops of the bulb-leaves) at the expense of its reserves. After the seeding is over the leaves continue to assimilate, and new reserve-stores are formed, but not in the original bulb. In the axils of the leaves buds are formed, and into these the reserves are carried, and the buds gradually enlarge into ' daughter-bulbs ' within the parent-bulb. Then when the latter dies down the new bulbs remain in its place.

Another type of shoot is the *corm* or ' solid bulb,' as seen in Crocus, Cyclamen, Colchicum, Eranthis, Bowiea, Testudinaria, &c. The lower part of the stem, at or below the level of the soil, is swollen out into a more or less spherical shape to contain reserve materials. At the top is the bud, which in the vegetative period forms the leafy shoot, at the expense of the reserves. In many cases new corms are formed as branches on the old ones and the latter have usually only one year's activity; the branches may be on top of the old corm (Crocus) or at the side (Eranthis, Colchicum). In other cases (Bowiea, Hablitzia, Testudinaria, &c.), the corm is perennial, and a new leafy shoot arises each year from the top of it, usually in the axil of a leaf of the preceding year. The corm is often (*e.g.* in Crocus) covered outside by a few membranous leaves, so that it looks like a true bulb till cut in section. The corm is simply a variety of the stem-tuber. The name *tuber* is given to any swollen part of a plant in which reserves are stored

up, except bulbs or leaves. The tuber may be of stem or root nature. In the former case it usually forms the termination of a special lateral branch, which grows out horizontally and swells up at the end. Underground tubers occur in potato (Solanum), artichoke (Helianthus), Ullucus, &c.; they betray their stem nature by their axillary origin (p. 33), and by bearing leaves reduced to scales, in whose axils buds ('eyes') are formed. These tubers subserve vegetative reproduction; the connecting branches die away and the eyes sprout out into new plants at the expense of the reserves. The main stem forms tubers in the cases of corms already mentioned, and in Dioscorea, Basellaceae, Tamus, epiphytic Orchidaceae, &c. Roots swollen into tubers occur in Dahlia, Thladiantha, Dioscorea, Bravoa, Paeonia, Uragoga, &c. In Orchis and other terrestrial orchids a bud forms in the axil of one of the lowest leaves; upon it is developed an adventitious root which grows into a tuber with the bud at its apex; this hibernates and grows out next year into a new plant, and so on. In dandelion (Taraxacum), Monotropa, Linaria, &c., the main root is fleshy and each new annual shoot arises at its summit, sometimes in the axil of one of the leaves of the preceding year, sometimes as an adventitious bud (see Pt. II.).

Again, we have the case of plants which store reserves in underground creeping stems or *rhizomes*. These are usually thickened; their leaves are reduced to scales, being useless for assimilation purposes. In a few cases the rhizome is monopodial (p. 35) and the leaves appear above ground, the stem remaining below, as in Pteris, but as a rule the rhizome is sympodial and each year's shoot is of an L shape, its upper end appearing above ground and producing green leaves. Rhizomes often branch largely, and as the older parts decay the branches are set free and thus vegetative multiplication occurs. Good examples of this form of shoot are seen in Iridaceae, Juncus, Musa, Dioscorea, Cyperaceae, Oxalis, Helleborus, Sanguinaria, and many other plants. In some cases the rhizome instead of creeping horizontally stands more or less erect and resembles a tuber; in such cases it is usually termed a *root-stock*. Aspidium is an example of such a rhizome with monopodial, Primula with

sympodial, structure.   All these types of stem graduate into one another by imperceptible stages.

Lastly, mention must be made of modified shoots whose chief or sole function is vegetative reproduction, rather than hibernation.   In Gesneraceae, short rhizomes or *suckers* are formed as branches which turn up at the end and form new plants ; these ultimately become detached from the parent plant. Creeping stems (*runners* or *stolons*) occur above ground in many plants ; they are usually formed as axillary branches on the main stem near the base ; they grow along the soil and take root at the nodes, and the axillary buds at the nodes form new plants.   This is well seen in the strawberry (Fragaria), Ranunculus sp., Agrostis, Agropyron sp., Epilobium sp., Nephrolepis, Ajuga, and others.   In Glaux, Samolus, Nasturtium, &c., new shoots are formed and take root, but can hardly be called runners.   The short runners of Sempervivum, Agave, &c., which bend up at the ends into new plants, are called *offsets*.

Vegetative reproduction is also common in the upper part of the stem, especially in the inflorescence portion, where some or even all of the flowers are replaced by bulbils, &c. (see p. 115).

Bud-protection (p. 33) is exhibited in many forms in herbs.   Those which have to survive a winter usually have their buds, as we have just seen, upon underground parts, and thus little further protection is required ; this is given by the formation of scales (modified leaves or stipules) on the outside of the bud.   Xerophytes and tropical plants, which require protection against drought and heat, are dealt with below.

Protection against grazing animals is obtained in many herbs by aid of stinging hairs (Urticaceae, Loasaceae, &c.), prickles, spines, &c., or by the presence in the tissues of poisonous or distasteful substances.   These also act as protections against snails, caterpillars, &c. (see Stahl's *Pflanzen und Schnecken*, Jena, 1889).   Glandular hairs also probably act as protections of this nature.

Shrubs and Trees.   These are perennial plants with woody stems above ground, and which do not entirely die down during the period when vegetation is interrupted. Shrubs are described as woody plants of not more than

about 30 feet high, and much branched down to the level of the ground, whereas trees have usually one stem at the base which branches out above, and generally grow to more than 30 feet in height. A sharp demarcation of the two classes cannot be made, all kinds of intermediate forms existing. Similarly between shrubs and herbs there occur intermediate forms; such low-growing shrubby plants as heather (Calluna) are termed *undershrubs*, and below these are suffruticose herbs (see above).

A very large proportion of the earth's surface is covered with trees and shrubs; in the colder parts of the north temperate zone these are mostly Conifers, elsewhere Angiosperms, or sometimes Ferns. Forests grow best where there is plenty of moisture, as in the tropical monsoon region, in the Amazon valley, and on the lower slopes of mountains.

The majority of trees and shrubs are *evergreen*, retaining their foliage throughout the year; others are *deciduous*, dropping their leaves in autumn or at the beginning of the dry season. In temperate climates the evergreens are chiefly Conifers, and the other woody plants are deciduous. The former are of monopodial growth (p. 35) and when growing apart from other trees are of more or less conical shape, with branches from top to bottom; in forests the lower shaded branches die and fall away and the tree spreads out at the top only. The deciduous trees usually show a more rounded shape when growing separately (*e.g.* elm or oak), and they do not generally show a single straight main stem reaching right to the top (*excurrent*) as in pines, but their stems are more or less broken up into branches (*deliquescent*) at some height from the ground. Most of them are of sympodial growth. In tropical regions most trees are evergreen. Two chief types occur, those with branched stems and those with columnar usually unbranched stems. The former branch in the ordinary way, but their branches very often grow almost erect and parallel, instead of spreading out in all directions, and the leaves are borne in rosettes or tufts at the ends of the twigs. The latter are best illustrated by the Palms, many Araliaceae, Cycads, &c., with an erect trunk bearing a rosette of large leaves. Both forms are excellently suited to growth

in forests, their leaves thus being all exposed to light at the top of the tree. In the dry climates of the sub-tropical regions many deciduous trees and shrubs are found, the leaves falling at the beginning of the dry period.

The woody plants of temperate climates form *winter-buds* (often even when evergreen, as seen in Rhododendron, &c.) at the ends of their branches in autumn; these contain all or part of the next year's growth in a more or less developed condition. The bud is exposed to evaporation, cold, wet, and other dangers, but is protected in most cases by scales; these are sometimes modified leaves, as in Acer, Aesculus, &c., sometimes the stipules of the outer leaves, as in Magnolia, Bucklandia, &c.; in some cases the scales are hairy, in others glandular or resinous, so that they form an efficient protection. In Juglandaceae, Viburnum, Sophora, &c. the winter-buds are not protected by scales, but their leaves themselves are more or less hairy or otherwise protected. Many winter-buds are able to absorb water from rain, and this helps them to recover their losses by evaporation at a period when the roots are not active.

In spring the winter-buds elongate, casting off their scales; the large buds of horse-chestnuts, pines, and other plants grow rapidly to their full elongation and then stop, so that the growth is *definite*, while in Rosa, Salix, Gleditschia and many other plants the growth continues till checked by the cold (*i.e.* is *indefinite*), the terminal part of the shoot dying and the new growth in spring starting from a lateral bud. In lilac (Syringa) and other plants the terminal bud regularly aborts and growth starts from the laterals in the succeeding year. The lateral buds in Robinia, Platanus, &c., are protected in summer by the bases of the leaf-stalks. Flower-buds also are often laid down in autumn, as seen in Prunus or Rhododendron.

The same principles apply to the resting-bud formation in desert plants, &c. The reserves necessary for the re-starting of growth are usually stored in the living cells of the stem.

The winter-buds of most trees and shrubs have characteristic sizes, shapes, colours, &c.; tables have been constructed for the determination of their genus and species from these characters (Plüss, *Unsere Bäume und Sträucher,*

Freiburg, 1894; Walser, *Der Baum im Winter*, Bern, 1894; Foerste in *Bot. Gazette*, 1892).

The fall of the leaves is usually effected by the formation of an *absciss layer* at the base of the stalk, cutting off the leaf-tissues from those of the stem by a development of cork (bark). This splits down the middle and leaves one half upon the stem, where it forms the *leaf-scar* covering the wound. Leaves thus cut off are termed *articulate;* those not thus cut off are *non-articulate*, as in the oak, whose leaves remain hanging upon the twigs most of the winter. The formation of the absciss layer is a definite vital phenomenon, as is seen in the case of broken branches, which, being deprived of their water supply and thus killed, do not form absciss layers.

Whilst in herbaceous plants all or most of the branch buds usually develope at once, this is not the case in trees. A number of the buds remain dormant and start into growth if the others be injured. Adventitious buds are often formed on the stems of trees and give rise to the leafy twigs seen on the trunks of elms, &c., and to the flowers borne on the trunks of many tropical trees, *e.g.* Ficus, Theobroma, Averrhoa. The *witches' brooms* so often seen in birch and other trees—bird's-nest-like bunches of twigs—are due to adventitious branching stimulated by the growth of a parasitic fungus (Aecidium) in the stem. Similarly the crown of branches of a pollard ash or willow arises from adventitious buds formed at the cut surfaces. At a wounded surface the cambium or formative tissue gives rise to a mass of *callus*, new cellular tissue covering the wound, and in this buds may develope.

The evergreen trees and shrubs of the damper tropical regions do not form resting-buds but vegetate all the year round, though commonly exhibiting a regular periodicity in the unfolding of new leaves, flowers, &c. The buds of young leaves require more or less protection from radiation and the accompanying dangers of too rapid evaporation or decomposition of the chlorophyll. A very frequent protective feature noticed in tropical plants is the red colour of the young leaves, well seen in Cinnamomum, Haematoxylon, Brownea, &c.; as the leaves get to their full size the chlorophyll developes. The young leaves commonly

hang downwards so that they receive less radiation (this may also be seen in Aesculus and other temperate plants), and straighten up as they become mature, *e.g.* in Bauhinia, Dryobalanops, Cinnamomum and many others. In Brownea, Amherstia, &c. the whole young shoot droops. In Artocarpus, Dipterocarpus, Ficus, &c. the stipules protect the bud; in Manihot the petioles of the young leaves curve upwards and inwards over the bud; in Tabernaemontana the bud is protected by the bases of the older leaves, which secrete a resinous substance, and so on (see Literature at end of chapter).

Many trees flower only at intervals, when they have saved enough reserve-materials to supply the flowers and seeds (cf. Agave, above). The beech is an example among deciduous trees; others, in tropical plants are Bambusa, &c., and the Arenga, Borassus and other palms which only flower once and then die.

As they grow in size, shrubs and trees grow in thickness in stem and root, usually by means of the cambium layer in the vascular bundles. A ring of wood is added each year to the older wood; the autumn and spring woods differ in texture and thus form a contrast, recognisable on a cut stem as an *annual ring*. Only the current year's wood is employed in the carriage of water up to the leaves; this, with the watery wood of the year or two preceding it, is termed the *sap-wood* or *alburnum* in contradistinction to the older *heart-wood* or *duramen*. The outside of the stem is covered by the *bark*, a corky layer formed by a special formative tissue or *phellogen;* between it and the wood lie the phloem and cambium.

Water-Plants. We have here to deal with a very well marked form of vegetation. Close similarity in the conditions of life seems to have determined, amongst plants belonging to various different families, a remarkable resemblance in general habit and structure. In few cases can we so satisfactorily determine which of the peculiarities with which we have to deal are really adaptations to the mode of life.

Primitive water-plants, *i.e.* those which have no land-forms among their ancestry, do not occur in the higher groups of plants with which this book deals, but only

among the Algae, &c. All the water-plants that are here
dealt with are undoubtedly descended from land forms, as
is indicated by their possession of flowers adapted (in most
cases) for pollination by wind or insects, and by many facts
in their morphology and anatomy. They probably began
as marsh plants and were gradually driven into purely
aquatic existence by the necessities of the struggle for
existence. The date at which the ancestral forms became
aquatic may have been comparatively recent or very far
back. In the latter case we find entire natural orders
composed of water plants, as Ceratophyllaceae, Naiadaceae,
Podostemaceae. In the former, we have instances like
Hottonia in Primulaceae, of one or two genera of a family
being aquatics, or such cases as the water Ranunculi, where
it is only one or two species in a genus. The modification
of structure to meet the changed conditions of life seems
also to have progressed, as a rule, more or less far according
to the presumable length of time the plants have been
aquatics. In the case of the orders first mentioned, a
study of the classificatory details will show how hard it is
even to decide upon their approximate position in a natural
scheme of classification. In the case of the water-plants
like Ranunculus, Potamogeton, and others of apparently
recent date, the variability is enormous and leads to extreme
difficulty in the determination of species, comparable only
to the cases of Rubus, Hieracium, &c. These plants having
only recently commenced their evolution into aquatics, it
has not yet become complete.

Let us now briefly consider the general conditions of
life and point out at the same time those peculiarities of
habit, external structure and internal anatomy which appear
to be in direct correlation to them.

In general the conditions of water life are far more
constant and uniform all over the world than those of exist-
ence on land. We find accordingly very few species of
spermaphytic water-plants and these have a far wider dis-
tribution than land-plants. Most of the British forms are
found throughout the north temperate zone. In the tropics
other forms occur, which not being interrupted either by
winter or by a dry season, vegetate continuously the year
round. In the temperate zones, on the other hand, hiberna-

tion is necessary. This may occur in a variety of ways. Ruppia, Zannichellia, Callitriche, Ceratophyllum and many others remain unaltered, though often sinking to the bottom of the water. Nymphaeaceae, *Potamogeton natans*, &c., hibernate in the form of rhizomes, stored with reserves to start growth in spring. *Potamogeton pectinatus*, Sagittaria, &c., form special tubers, something like the potato. A large number form special winter-buds—large buds at the ends of the stems, with a great number of closely packed green leaves provided with reserve food-stuffs. These usually drop off and spend the winter at the bottom of the pond, coming up and expanding in spring. Such are Utricularia, Hottonia, Myriophyllum, Hydrocharis, *Potamogeton crispus* and other species. More or less unique methods of hibernation occur in Lemnaceae, &c. (*q.v.*).

Owing to the high specific and latent heats of water, a water-plant is less exposed to violent changes of temperature than a land-plant, and if there be plenty of water, is not liable to be interrupted in its growth by a drought in summer, as so often happens to land-plants even in temperate regions. These conditions favour its vegetative growth considerably, and it is still more aided by the peculiar conditions of nutrition. A water-plant takes in all or most of its food in solution from the surrounding medium, which contains, owing to the difference in solubility of the two gases, more carbon dioxide and less oxygen in proportion than does the air. As the latter contains more oxygen than is needful, and less carbon dioxide than would be most advantageous to vegetation, it may be seen that the water-plant is highly favoured. Correlated with these things is the exceedingly rapid growth, frequent branching, and extensive vegetative reproduction exhibited by water-plants. This last occurs to some extent in the formation of several winter buds or tubers on a single plant ; it happens also by the decaying away of the older parts of stems and the consequent liberation of the branches, which is seen in so many water-plants, or even by the breaking off of twigs by currents of water or otherwise (as occurs so constantly in Elodea), and in other ways.

Correlated with the fact that all submerged parts absorb fluid directly is the absence of cuticle on the surface and

the branching of leaves, &c. to expose a large area. Partly owing to this and partly to the fact that there is no tran- spiration in submerged plants, there are few or no stomata and little or no water-carrying tissue present (xylem-vessels or tracheids), and the root-system, deprived of one of its great functions, is either absent altogether or very much reduced, serving only for anchorage of the plant.

Again, mechanical influences come into play. An ordinary stem or leaf requires, as we have seen, a quantity of "mechanical tissue" (fibres) so disposed as to resist the various stresses caused by weight, wind, and so on. In a water-plant, the weight is upheld by the water and there is no need for mechanical tissue in the plant itself, nor do we find it. What little strain there is on the stem, &c. is usually longitudinal, and the vascular bundle (the strongest tissue of the plant) is axially placed, as in a land-root, to resist it. The leaf exhibits four main types, according to the conditions under which it lives, *viz.* (1) the ribbon type, (2) the much-divided type, and (3) the awl-shaped type in submerged leaves, and (4) the floating type. The first is seen in most Monocotyledons, *e.g.* Vallisneria, Glyceria, Potamogeton sp. &c.—the narrow leaf drifting with the current in the form of a long ribbon. This type of leaf is apparently the primitive one in the Monocotyledons, if we may accept as evidence the fact of its frequency in the seedling-leaves (p. 113). It is interesting therefore to see it in water-plants, which exhibit a low type of organization in many ways; it may be regarded as a case of reversion to ancestral type, or perhaps more probably as a case of hindered development. The much-divided leaf, with linear segments, is seen in Ranunculus, Cabomba, Trapa, &c.; special patterns that also belong to this class are the leaves of *Aponogeton fenestralis* and others. Hippuris may form a link between this group and the preceding. The awl-shaped leaf is found in Isoetes, Subularia, Lobelia, &c.; most of these plants are able to grow on dry land, usually in other forms more suited to land-existence. The floating leaf, as seen in Nymphaeaceae, Trapa, Ranunculus sp., &c., is usually large, entire or nearly so (a divided leaf would be easily submerged, or at least wetted so as to interfere with its functions), of leathery consistency and usually of oval

or circular outline. The stalk is capable of renewing its growth should the leaf be submerged, so as to bring it back to the surface. The upper surface of such a leaf is provided with cuticle (often waxy), palisade-tissue and stomata, and functions like a land-leaf.

Another determining factor in the structure of water-plants is light. Water absorbs it to such an extent that submerged plants are practically shade-plants (p. 152) and exhibit similar features. The internodes of the stem are long (etiolated; *cf.* climbing-plants, below), the leaves are usually thin and have no palisade-tissue, and the cells of the epidermis contain chlorophyll.

. A very characteristic feature of water-plants is the presence of enormous intercellular spaces, giving the tissues a spongy consistency easily visible to the naked eye. They are full of air and probably serve more than one function; they act as floats to the plant, they probably aid in the assimilatory functions by supplying gases to the cells, and they also seem to act as channels by which oxygen can reach those parts of the plant which are in deep water or in mud where there is little or no oxygen for respiration. In this last connection it is interesting to note that secondary respiratory tissue (*aerenchyma*), formed by the phellogen layer, is frequently found, *e.g.* in roots of Sesbania and Jussieua, stems of Neptunia, &c. It also appears in mangroves (see below), Taxodium, and other mud-plants, and is said to occur on submerged parts of Lycopus, Lythrum, &c. (see also Rumex). The intercellular spaces above-mentioned also occur in marsh-plants and are therefore hardly to be regarded as adaptations to an aquatic life.

One of the most common structural peculiarities of water-plants, whether Algae or higher plants, is their sliminess. In the flowering plants it is usually due to a secretion of mucilage by glands or hairs upon the surface. Its presence renders diffusion more slow and is probably advantageous in this way, by preventing the too rapid escape of the substances dissolved in the cell-sap into the surrounding water. Whether this is the explanation of the presence and use of the mucilage is another question.

Most water plants are perennials; annuals occur in the genera Naias, Subularia, Marsilea.

The great vegetative growth and multiplication of water-plants is accompanied as usual (p. 100) by a reduction of the flowering activity. Many species rarely flower, and very few flower as profusely as land-plants. Most species display their flowers above the water for pollination by wind or insects. The mechanisms resemble those of ordinary land-plants, but the flowers are rarely successful in setting much cross-fertilised seed, for they are so close to the water that much of the pollen of the anemophilous species falls into the water and is wasted, and insects are few and far between so that the entomophilous species are not much visited. A few plants, *e.g.* Elodea and Vallisneria, display a modification of their floral structure adapted to pollination at the surface of the water, and in Ruppia, Zostera, &c., pollination takes place under water and the floral structure is highly modified (see Pt. II.).

The fruits are usually achenes, nuts, or schizocarps, and are nearly always ripened under water; some plants, *e.g.* Vallisneria, have special arrangements for drawing them down to ripen (*cf.* Cyclamen). The seeds (or fruits) usually sink in water, but some plants have arrangements by which they may be kept afloat for a time and thus dispersed to a distance (see Nymphaeaceae, &c.). The germination of the seeds often furnishes interesting features—leaves differing from those of the mature plant, special adaptations, &c.

The various characters of water-plants are separated in the above analysis, but in reality many or most of them occur together in each plant. The same plant may often grow at different times under different conditions and exhibit different structural features and habit. Many of the plants which usually grow in marshy places are able to grow submerged in water, and frequently the land and water forms differ, *e.g.* in Littorella, Polygonum sp., &c. Such plants may be termed *amphibious*. The most fully adapted water-plants, such as Myriophyllum, Vallisneria, Zostera, &c., are not capable of living upon land.

A wide-spread phenomenon is *heterophylly*, or the production of two or more kinds of leaves on the same plant, *e.g.* swimming leaves and submerged leaves, of the patterns described above. Examples are Cabomba, Callitriche, Potamogeton sp., Ranunculus sp., Sagittaria, Salvinia, Trapa, &c.

For further details reference should be made to Pt. II, articles Aldrovanda, Alismaceae, Aponogeton, Azolla, Bidens, Cabomba, Callitriche, Ceratophyllum, Eichhornia, Elodea, Jussieua, Lemna, Littorella, Limnanthemum, Myriophyllum, Naias, Nelumbium, Nuphar, Nymphaea, Nymphaeaceae, Peplis, Pistia, Potamogeton, Potamogetonaceae, Ranunculus, Rumex, Ruppia, Sagittaria, Salvinia, Sesbania, Stratiotes, Subularia, Trapa, Vallisneria, Victoria, Zannichellia, Zostera, &c.   See also Literature at end of chapter.

Climbing Plants.   Here again we have a group founded upon a biological peculiarity and including plants of very many different families of flowering plants and ferns. They occur in all parts of the globe, but abound especially in tropical forests, where they form a characteristic feature of the vegetation.   The climbing plant throws its weight upon an external support, and thus evades the necessity of forming a rigid stem capable of standing by itself.   Now we know (p. 36) that the great bulk of an erect stem consists of fibres, whose function is purely mechanical.   Comparatively few of these are produced in a climbing plant, and its growth in length is correspondingly more rapid, so that it is able to reach the full daylight very much sooner than an erect plant. In a dense tropical forest this is a point of very great importance to the species, and even in temperate climates many herbaceous plants owe much of their success to the possession of this habit.

Darwin (*Climbing Plants*) divides these plants into four groups, with which we shall briefly deal, giving numerous examples, for details of which reference must be made to Pt. II. and to the literature of the subject.

I. *Twining Plants.*   These plants climb by twining round their supports, as may be seen in hop or bindweed.   The support must not be very thick nor very smooth, and must stand more or less upright, otherwise the stems are not able to twine.   Twiners exhibit many of the characters of etiolated plants (p. 40); they have long thin stems, with nodes far apart, and the growing and elongating part at the tip is very long, and shows very marked nutation in consequence (p. 41).   The nutating tip of a twining stem may describe quite a large circle, even several feet in diameter.   This gives of course a much better chance of finding a support.   Plants

of this kind are usually supposed to have been evolved in the shade of forests or other vegetation, the etiolation-characters thus produced gradually leading to a twining habit and becoming hereditarily fixed. The actual mechanism of twining is not clearly understood. Nutation alone would tend to make a stem twine, for when the nutating part struck against a support, the point of contact would become a new centre of nutation; but this is not sufficient to account for the steep loose spiral which is formed by a twiner, for it would tend probably to make the stem twine in a close nearly horizontal spiral. The aid of negative geotropism, which is strongly marked in many twiners, is therefore invoked to account for the comparatively erect position of the stem, but we cannot clearly explain the exact mechanism of the process.

The spiral may be right or left-handed; the same plant or species usually twines throughout in the same way. The direction may be defined as clockwise, *i.e.* in the direction of the hands of a clock, or counter-clockwise; the terms right and left are used in opposite senses by different writers. At the same time that it twines round the support, the stem usually becomes twisted upon its own axis, but there is no relation between the number of turns of the spiral and the number of twists.

The length of the internodes is usually sufficient to ensure the leaves not overlapping each other, and no special forms of phyllotaxis are found.

In the British flora twiners occur in the genera Tamus, Humulus, Aristolochia, Polygonum, Calystegia, Convolvulus, Cuscuta (this genus has sensitive stems, like tendrils), Solanum, Lonicera. Other genera of interest are Lygodium (fern with twining midrib of leaf), Ruscus, Cassytha, many Lardizabalaceae, Menispermaceae, and Malpighiaceae, Wistaria, Phaseolus, many Loasaceae and Combretaceae, Plumbago, Dipladenia, Cynanchum, Ceropegia, Hoya, Ipomœa, Thunbergia, Mikania, &c. Many of these have hooks on the stem, aiding them in clinging to their supports, *e.g.* Humulus, Dipladenia.

II. *Climbers with sensitive organs.* The plants of this group are characterised by the possession of organs which are sensitive to continued contact and which move in response

to this stimulus. As in all cases of adaptation, the most various parts have become adapted to this end. In the majority of these plants the organs are *tendrils ;* the typical tendril is a long thread-like structure with rapid growth and marked nutation. If it come into contact with a support, the stimulus causes the side away from the support to grow more rapidly than the one touching it, and thus the tendril curves towards the support. This brings a new surface into contact with the support and the movement becomes more marked, and so on until the free end of the tendril is all wound round the support. If this were all, the organ would not be very much support to the stem, and would be easily broken in strong winds, &c.; but after clasping the support the free portion of the tendril twists into a spiral and becomes lignified, thus forming a firm but elastic support, and at the same time dragging the stem upwards and thus economising its materials. The direction of the twist reverses at some point in the spiral ; this has often been regarded as an adaptation to prevent the tendril becoming too much twisted on its own axis, but in reality it is a mere mechanical result of the spiral twist. If an attempt be made to twist a piece of wire, fast at both ends, into a spiral, it will be found necessary to reverse the twist at the middle.

Some tendrils, *e.g.* those of Vitis sp., have adhesive discs at the end, others, *e.g.* those of Cobaea, hooks.

Tendrils, morphologically considered, may be of various nature—stems (usually modified inflorescence-axes), leaves or parts of leaves, or even roots. The aerial roots of Vanilla and perhaps other plants may act as tendrils; modified stipules form the tendrils of Smilax, &c., modified leaves or parts of leaves of many Leguminosae (*e.g.* Lathyrus, Vicia, &c.), Bignoniaceae (*e.g.* Bignonia) and Cucurbitaceae, Mutisia, Cobaea, Corydalis, &c.; modified stem-structures forming simple tendrils occur in Vitis, Passiflora, Antigonon, Landolphia, &c. A special form of tendril is the sensitive hook that occurs in so many tropical climbers. Inflorescence-axes, modified in structure to form recurved hooks, project from the stem ; when a hook catches a support, it clasps it tightly and becomes lignified. Such hooks are found in Artabotrys, Hugonia, Uvaria, Ourouparia, Unona, Ancistro-cladus, Landolphia, Strychnos, Uncaria, &c. Sometimes

they are long, thin and flat, and are rolled up like watch-springs, as may be seen in some Sapindaceae (Paullinia, &c.), Gouania, Bauhinia, &c.

Many plants climb by aid of sensitive leaves. In Gloriosa, Littonia, &c., the tip of the leaf is sensitive, acting like a tendril. The petiole is often sensitive to contact, clasping as a rule however only once round its support, and then frequently becoming lignified. Such cases are found in Tropaeolum, Clematis, Hablitzia, Maurandia, Rhodochiton, &c. Mention may also be made of the leaf-climbers, Fumaria, Adlumia, and Nepenthes (see Pt. II).

Other plants climb by aid of sensitive lateral branches, which bear ordinary leaves. Such occur in the genera Securidaca, Hippocratea, Uvaria, Salacia, Machaerium, &c. Sometimes the branches are leafless and tendril-like, but they are always capable of producing leaves.

III. *Hook-climbers.* To this group belong those plants which merely sprawl over other vegetation, and have hooks, usually recurved, which aid in their support. The only British hook-climbers are Galium and Rubus, both of them with small hooks arising as mere emergences (p. 116); in the tropics many hook-climbers grow to a great size and have stem- or leaf-structures modified into hooks, *e.g.* Calamus, Desmoncus, Caesalpinia; to these may be added species of Rosa, Pereskia, Capparis, Lycium, &c. These hooks are not sensitive to contact like those described in the preceding section.

IV. *Root-climbers.* A number of plants climb by aid of special roots produced upon the stems (adventitious). These roots are not usually sensitive to gravity but show a marked negative heliotropism (p. 21), which causes them in their growth to follow out all the crannies and irregularities of the surface upon which they creep, and thus to firmly attach themselves to it. Instances are found in ivy (Hedera), many Araceae, Hoya, Tecoma, Norantea, Ficus sp., Piper sp., and many ferns. The aerial roots of Philodendron sp. twine as they descend. Ivy and others have dimorphic shoots (*cf.* Salacia, &c.).

The general external characters of climbing plants are sufficiently indicated above. Anatomically they present many features of interest. The stem is very thin compared

to its length, but grows slowly in thickness to supply the new leaves with water. The growth is commonly 'abnormal' and results in many cases of tropical climbers (lianes) in stems of the most remarkable shapes—flat, twisted, corrugated, &c.—which may be seen in most museums. For further details see Pt. II. and Literature at end of chapter.

Xerophytes. In such a climate as that of the lowlands of western Europe, everything in the structure of the leaf, the phyllotaxy, branching, &c., is so arranged as to favour transpiration to the utmost, and thus to cause a rapid current of water from the roots to the leaves. So long as the roots can absorb plenty of water this form of plant-organisation is an excellent one, and the rapid absorption of materials favours rapid growth. But if the roots are not able to absorb water at all times fast enough for so much evaporation, it is evident that a reduction of the transpiration is a prime necessity of life, and that plants in which this is effected will be most suitable to such a position or climate. These conditions occur in many places— in countries with long dry seasons when the water supply runs short, in arctic and high mountain regions where everything favours transpiration (see below) and the coldness of the soil checks absorption (p. 41), in sandy or rocky soils, upon sea-shores or in salt steppes where the presence of salt in the soil renders absorption difficult, in epiphytic situations (see below) and also in winter when the soil is too cold for absorption. In all such places the plants show a remarkable general similarity, and agree in having a lower rate of transpiration than plants living where there is plenty of available water. Plants of this kind are termed *xerophytes;* etymologically the name is not altogether suitable, as many of them live in very wet places, but it is a convenient term for general use. We shall deal in this section with the general features of xerophytes, with particular reference to those of dry climates ; epiphytes, shore-plants, alpine plants, &c., are treated below.

As so often happens, a compromise has to be made between opposing necessities—the need of reducing evaporation, and the need of vigorous assimilation. The structural features that favour transpiration favour assimilation also, and the reduction of the former tends to be accompanied

by that of the latter function. Every possible compromise may be seen in the variety of structure found in xerophytes.

All round the world, in the sub-tropical regions, there are vast areas in which there is a long rainless season in the year. Such are the Mediterranean region. Arabia, the Steppes of Asiatic Russia, the desert of Gobi, the southern prairies of North America, Mexico, Peru, Chili, the Pampas, much of South Africa and Australia. In all these regions xerophytes occur, their perfection of adaptation depending on the length of the dry season. If the drought be not very prolonged, many xerophytes are able to survive by the mere reduction of the transpiration, but if it be extreme, or last for a long period, water is stored up to enable the plants to survive, and they are more or less fleshy in structure. In this case other materials are often stored also, and vegetation stops during the drought, to be resumed with the wet season.

We shall now briefly describe the chief structural features by which transpiration is reduced; for details see Pt. II, and Literature (end of chapter).

An almost universal feature in xerophytes is a thick cuticle upon the epidermis of the leaf (p. 25); an ordinary epidermis has only a thin cuticle, through which a considerable amount of evaporation goes on. The leathery texture of the leaves of many xerophytes is partly due to the thickness of their cuticle.

The number of the stomata upon the leaf is commonly very much reduced, and also the size of the intercellular spaces in the interior of the leaf; in this way evaporation is much lessened. Instead of being flush with the surface the stomata are commonly sunk at the base of small pits in the leaf, into which the wind cannot enter, and which therefore become filled with saturated air, thus reducing transpiration. In Pinus, Aloe, and most xerophytes there is a separate small pit for each stoma, but in Nerium and others the pits are large and contain several stomata. A somewhat similar arrangement on the large scale is seen in the grooves of such leaves as those of Empetrum, Vaccinium sp., Phylica, Cassiope, Rosmarinus, or such stems as those of Casuarina, Spartium, Cacti, &c., the stomata being at the bottom of the furrows. The grooves are more or less covered in in

the leaves mentioned, especially in Empetrum; in many of the grasses (*e.g.* Stipa) the leaf rolls up in dry air, completely closing in the stomata, and exposing only the impervious surface to the outer air.

The surface of xerophytes is often clothed with a thick covering of hairs, which retard transpiration by preventing the wind from reaching the stomata. This is well seen in the Edelweiss, in many alpine willows, in Stachys sp., *Alchemilla alpina,* Helichrysum, &c. A covering of wax occurs on the epidermis of many Liliaceae (*e.g.* Aloe), Crassulaceae, &c., a covering of silica on that of *Crassula (Rochea) falcata.*

The thick sap of such plants as Aloe is another preventive against excessive transpiration, for it only evaporates very slowly.

Instead of being spread out to the utmost extent to prevent overlapping and shading of one another, the leaves of many xerophytes are closely placed on the stems and overlap one another very much. This is well seen in Gasteria, Aloe, many Crassulaceae, Calluna, &c. The plants often grow in dense tufts, closely crowded together, and thus further reduce the free access of air and check evaporation. Raoulia and Azorella are good instances; the phenomenon is especially frequent in alpine plants.

Comparatively rarely are the structural features above described sufficient to enable the plant to survive the dry season in hot climates, though they are frequently all that is necessary in alpine or arctic plants, or in evergreen temperate plants. Further arrangements for reduction of transpiration occur in most xerophytes; these may be grouped under a few heads, as follows. We shall deal first with evergreens, to which group most xerophytes belong.

The most simple mode of reducing evaporation is a reduction of the transpiring surface, which is very common. The leaves of Hakea sp., Grevillea and other Proteaceae, *Rubus australis,* Russelia, &c., are much branched, like those of water-plants, into fine segments which expose but little surface for evaporation. Comparison with related forms or observation of seedlings (p. 113) shows in most of these cases that a real reduction of leaf-surface has occurred

in the course of ages. In many Ericaceae the leaves are narrow and needle-like, and often more or less rolled back, and this *ericoid* type of leaf is found in many xerophytes, *e.g.* Aspalathus, Epacridaceae, Empetraceae, many Rutaceae (*e.g.* Diosma), Rhamnaceae, &c.; a somewhat similar form occurs in Ulex, and in Pinus and other Conifers. The leaves of Cupressus and other Conifers are reduced to small green scales and closely pressed against the stem; this form is remarkably imitated in many alpine species of Veronica from New Zealand, and in other xerophytes. In these cases the stem usually does some of the assimilation, and a further progress in this direction leads to cases in which all the green tissue is found in the stem and the leaves are reduced to scales. Stems of this kind, still retaining their more or less cylindrical form, occur in Casuarina, Cytisus sp., Spartium, Baccharis, Restio, Juncus, Ephedra, &c. They are usually grooved lengthwise, and the green tissue and stomata occupy the bases of the grooves. In some species of Baccharis, Genista, and others, the green stems have their assimilating surface increased by the presence of longitudinal wings; this leads on to such cases as Bossiaea, Carmichaelia, Muehlenbeckia, Phyllanthus, &c., with long shoots transformed into flat green expansions, which act as leaves, whilst the true leaves are reduced to scales. Such stems are termed *phylloclades;* they occur also in Ruscus, Semele, &c., as short lateral branches, closely resembling leaves (see also Colletia). Standing with their edges to the sky they transpire much less than a leaf of similar size which places its flat surface to the sky.

This advantage of phylloclades—the edgewise position—is also obtained in many xerophytes which possess green leaves. In many tropical Leguminosae, &c., the leaves (or leaflets) move upwards or downwards when the radiation becomes too intense, and thus expose only their edges or at most sloping surfaces to it (*cf.* sleep-movements, p. 30). In the compass-plants Lactuca and Silphium (*q.v.*) the leaves stand edgewise in such a way as to obtain the full radiation of the morning and evening sun. In Eucalyptus and many other xerophytes the leaves are more or less twisted at the base, so as to place their edges upwards. The *phyllodes* of Acacia (*q.v.*) &c., attain the same end in a different way.

Another similar adaptation is seen in the isobilateral leaves of Iris, Narthecium, Phormium, &c., and the centric leaves of Juncus, &c. (p. 30).

In addition to the reduction of transpiration obtained by the methods above described many xerophytes store up water to last them through the dry season, and thus become more or less succulent. The water is usually stored in *aqueous tissue*, consisting of large colourless living cells. Often this tissue forms a layer between the upper epidermis of the leaf and the palisade-tissue, as in Aeschynanthus, Peperomia, &c. More extreme development of the storage-function leads to the true *succulent* plants. The storage may be in the leaf, as in most Crassulaceae, many Liliaceae (*e.g.* Aloe, Haworthia, Gasteria, &c.), Aizoaceae (*e.g.* Mesembryanthemum), Drymoglossum, Agave, Fourcroya, Sansevieria, &c., or in the stem, as in Cactaceae, many Asclepiadaceae (*e.g.* Stapelia, Huernia, Sarcostemma, Ceropegia, &c.), Euphorbia sp., Senecio sp., Sarcocaulon, Salicornia, &c. In the leaf-succulents the leaves are thick and fleshy, are usually closely packed, and provided with thick cuticle, sunk stomata, &c. In the stem-succulents the leaves are reduced to scales or thorns; the stems are fleshy and of various shapes (see Pt. II.), and are often grooved. Many of these succulents, especially the Cacti, are able to survive very protracted drought. It is very difficult to dry specimens for the herbarium. They do not, however, resist long-continued wet weather easily, but soon decay.

Besides the evergreen xerophytes that we have just considered there are a great many species which vegetate only during the wet season and die down or drop their leaves in the dry season. Annual species, which exist only as seeds during the drought, are common. Anastatica is one of the best known. Bulbous plants (p. 162) are abundant in many of the regions mentioned above, *e.g.* in California, South Africa, &c. Other perennials have underground storage in tubers, *e.g.* Bowiea, Testudinaria, &c.; when the tuber, as in the latter genus, projects above the soil it is usually protected by a thick bark. Thick roots occur in other xerophytes, and so on. Many shrubs and trees drop their leaves in the dry season and store reserves to start growth when the rains begin. The "Catinga" forests of Brazil consist

chiefly of species of this kind; many Bombacaceae, Jatropha, &c., are examples. They are usually well protected by thick bark and have deeply-penetrating roots.

Xerophytes show in general, as might be expected, the characters of sun-plants (p. 152), *e.g.* a very well-developed palisade-tissue, thick leaf, &c. The wood is usually hard, dry, and brittle. Many, especially the desert species, are thorny, *e.g.* Alhagi, Acanthophyllum, Acantholimon, Astragalus, Euphorbia, Cactaceae, &c. The thorns are probably useful as protections against animals, especially in the more succulent species.

Bud-protection against extreme heat and excessive transpiration is well marked in most xerophytes. In the succulent forms, *e.g.* Mesembryanthemum, Aloe, Agave, Cactaceae, the bud is usually deeply sunk among the leaves or in a groove or pit in the stem, so that it is almost completely covered. Other protections, of the various kinds already described, occur in other species. The dry-season buds of non-evergreen species show protections like those of winter-buds.

The flowers are often produced in the dry season, or at the beginning of it, or during the drier parts of the wet season, and many have bud-protections, *e.g.* Eucalyptus and other Myrtaceae. The conspicuousness of the flower is often aided by, or entirely due to, the stamens, as in Acacia, Callistemon, &c.; there is not much risk of the pollen being spoiled by rain, and hence the protections found in flowers of wetter climates are not necessary here. Other flowers that freely expose their pollen are Grevillea and most other Proteaceae, &c.

The seeds of many xerophytes are exposed to severe drought before the rains come on, and require good protection. Those of many Proteaceae (*e.g.* Banksia, Xylomelum), of Eucalyptus, Casuarina, &c., are enclosed in hard, woody fruits. Many are enclosed in fruits which only open when wetted (the reverse of the usual behaviour of fruits, see p. 112); such are Anastatica, Mesembryanthemum, Odontospermum, &c.

Further details will be found in Pt. II.; see the orders and genera mentioned above, and Velloziaceae, Cheilanthes, Espeletia, Dasylirion, Lewisia, &c. See also the Literature at end of chapter.

Epiphytes. These are plants which grow clinging to other plants for support, but are not parasitic upon them, and are not usually attached to the soil. In the temperate zones they are rare—a few Algae, Mosses and Liverworts commonly live in this way—but in the wetter (forest) regions of the tropics they abound, forming one of the most marked features in the vegetation; they occur in great numbers in Brazil, Java, &c., perched upon the branches and even leaves of other trees and plants. Being themselves usually small herbs they thus obtain favourable situations for themselves without the expenditure on stems needed by erect plants and even by climbers, but on the other hand they are placed in positions in which the obtaining of food (except carbon) becomes much more difficult than to plants with terrestrial roots. They form a good group of plants in which to study adaptation; they are excellently suited, most of them, in structure and physiology to their mode of life, and yet they possess few or in some cases no true adaptations to it. The group is made up of a number of genera which happen to possess in common a number of characters—adaptations to various ends—which enable their possessors to become epiphytic. The ferns, Bromeliaceae, Orchidaceae and Araceae are largely represented in the group; important genera of epiphytes, not belonging to these families, are Piper, Clusia, Phyllocactus, Rhipsalis, Columnea, Dischidia, Aeschynanthus, Hydnophytum, Myrmecodia, &c.

In the first place, no plant can become epiphytic unless it has an excellent seed-dispersal mechanism. Wind and birds are the only agents capable of regularly carrying the seeds to sufficient heights. All epiphytes possess either wind or bird mechanisms. Interesting observations may be made on this part of the subject by studying the flora of pollard trees in Europe; in the bowls of humus at the tops of willows, &c. many species occur. Numerous papers on these have recently been published, and though the composition of the epiphytic flora varies with that of the region studied, the proportion of wind- and animal-dispersed species is much the same in all, viz. about 55 °/$_o$ of the former and 30 °/$_o$ of the latter; only about 15 °/$_o$ of the species (3 °/$_o$ of the individuals) have mechanisms incapable

of transporting their seeds to the requisite height, and of these many are carried up, more or less accidentally, by birds in nest-making (see Literature at end of chapter). Whilst the wind-dispersed species are more numerous than the animal-dispersed the reverse is the case with regard to the number of individuals; and the same rule seems to hold good with true epiphytes, *e.g.* the wind-dispersed Orchidaceae have more species of epiphytes, but fewer individuals, than the animal-dispersed Bromeliaceae.

In the second place, a species to become a successful epiphyte must be able to fasten itself to its support, and that at once after germination. Just as in Europe plants with good dispersal-methods may become epiphytes in willows, where there is plenty of food and no difficulty in anchorage, so in the tropics many become more or less accidental epiphytes in the leaf-sheaths of Palms, &c., or in the pitchers of Bromeliaceae, and so on. True epiphytes however are able to cling to almost any support at any angle, and they do this usually by means of clasping roots of the kind found in ivy and other root-climbers (p. 177). It is noteworthy that such roots are always adventitious, developed from the stem; now it is necessary that the germinating seed should be promptly fastened to its support, and in Monocotyledons these adventitious roots are produced very early (p. 24) in germination, and thus we can perhaps understand why Monocotyledons form so large a proportion of the epiphytic flora. Tap-rooting plants, as so many of the Dicotyledons are, would not be able to cling to their supports in time to prevent falling off. One group of epiphytes, the Araceae (*q.v.*), seems to have been evolved from plants which originally climbed with clasping roots.

In the third place, epiphytes are placed in conditions where the water-supply is small and precarious and easily runs away. No plants then can be regular epiphytes unless they possess well-marked xerophytic characters, including as a rule the capacity for water-storage. The Orchidaceae collect water by their aerial roots and store it in tubers or fleshy leaves; Bromeliaceae have fleshy leaves and water-collecting pitchers; ferns have fleshy stems and also gather much humus which retains water well; 'aqueous tissue' in

which water is stored occurs in the leaves of Aeschynanthus, Peperomia, &c.; other arrangements occur in other species. A peculiar case of semi-epiphytism occurs in many Araceae (*q.v.*) which have long nutritive roots descending to the soil; the same thing is seen in species of Clusia and Ficus.

Not merely is there difficulty in getting water, but also the mineral substances required for nutrition. Most epiphytes obtain these from decaying organic matter (*humus*), and many have interesting arrangements for its collection. In most forms a certain amount of dead leaves and other *débris* collects at the base of the plant; in many ferns the leaves make niches against the support, *e.g.* in Polypodium sp. and Platycerium, or form nests, as in *Asplenium nidus;* in Dischidia the pitchers collect humus, and also in Bromeliaceae. Details must be sought in Pt. II.

We have seen that in Europe epiphytes only occur in moist places, and moisture seems everywhere an important factor in regulating their distribution. In the deep ravine below the Devil's Bridge, in Cardiganshire, the trees may be seen loaded with epiphytic ferns, &c. Plants living on the soil in a tropical forest may similarly become epiphytic to this extent if they possess the necessary methods for seed-dispersal and anchorage of the seedlings. They may then gradually work higher up the trees, and thus get nearer to the light as they develope xerophytic characters sufficiently marked to enable them to stand the increased tendency to transpiration, and so on. In actual fact we find epiphytes with very pronounced xerophily on the very tops of trees, others with less marked characters lower down. On the savannahs of America, where the climate is drier, the species from the tops of the forest trees occur as epiphytes, but no others. These well-marked epiphytic species also occur as alpine forms in neighbouring mountains, but not in the intermediate zone. This is easily understood, as they are equally well adapted for this form of life. So also they become shore-plants.

For further details see Pt. II., especially articles Polypodium, Platycerium, Bromeliaceae, Tillandsia, Araceae, Orchidaceae, Vanilla, Oncidium, Bulbophyllum, Scuticaria, Phalaenopsis, Clusia, Ficus, Marcgravia, Dischidia, Rhododendron, Myrmecodia; also Literature at end of chapter.

Sea-coast and Salt-steppe Plants. We have mentioned above that plants living where the soil contains much salt exhibit xerophytic characters; the presence of the salt renders absorption of water by the roots slow, and thus there is less available for transpiration, and at the same time its presence in the assimilating cells checks the process of assimilation and may even stop it altogether or kill the plant if the concentration become too great. It is therefore evident that a reduction of transpiration is a prime necessity to such plants. Besides those plants which live close to the water and therefore find much salt in the soil, there are also many plants that grow on sand-dunes a little way back from the sea; here there is less salt but the soil is not retentive of water, and therefore there is a necessity for reduction of transpiration. To these groups may be added the plants of salt steppes, which show similar habit and structure to the true shore-plants. All plants living in salt soil are often classed together as *halophytes.* The group is composed of members of many natural orders; the Chenopodiaceae, Aizoaceae, Plumbaginaceae. Rhizophoraceae, Frankeniaceae, &c., consist chiefly of halophytes. We shall deal first of all with the coast vegetation as seen in Britain and western Europe, and then with that of more southern regions.

The coast-flora of Britain, &c., varies according to the nature of the soil, whether rock, sand, or mud. Upon rocks we find such plants as *Crithmum maritimum, Silene maritima,* &c. The flora of a sandy coast varies according to the distance from the sea. On the sandy shore itself, where the soil is saturated with salt water at a small depth, but is liable to become very hot and dry at the surface, occur such plants as *Cakile maritima, Salsola kali,* species of Atriplex, *Arenaria peploides, Calystegia soldanella,* Crambe, Mertensia, *Glaucium flavum, Eryngium maritimum,* &c.; these are mostly annuals, or perennials with creeping stems, or long tap-roots by which they are firmly anchored to the soil. All these plants are more or less fleshy, and show other xerophytic characters (sunk stomata, thick cuticle, wax, &c.) as well. A little further back from the sea the region of sand-dunes begins; those close to the shore are always shifting under the action of the wind, and only those plants occur upon them that besides being xerophytes are able to

come up again if buried by the sand (the formation of dunes is chiefly due to the growth of these plants) and which possess good anchorage. Such are the grasses *Ammophila arundinacea* and *Elymus arenaria*, with long rhizomes and often with leaves which roll up in dry air (p. 180). *Carex arenaria*, *Hippophae rhamnoides* and other plants may also occur here. The growth of these plants gradually binds the dunes together, and further inland they form a sufficiently stable soil for the growth of such plants as *Carex arenaria*, species of Festuca, Ononis, *Lotus corniculatus*, *Galium verum*, *Sedum acre*, *Antennaria dioica*, Thymus, and frequently Erica and Calluna. These also show more or less marked xerophily; the shore forms of Lotus and other inland species are fleshy, and a few other succulents occur, but most of these plants reduce transpiration in other ways. Lastly, where the shore is muddy, as in estuaries, a somewhat different flora appears. Farthest out occur masses of Zostera, then *Salicornia herbacea ;* both of these are entirely submerged at high water. Further inland, out of reach of most tides, where the ground is firmer, occur *Glyceria maritima*, *Triglochin maritimum*, *Plantago maritima*, *Suaeda maritima*, Glaux, Statice, Cochlearia, *Spergularia marina*, *Aster tripolium*, &c. Higher up still many of these disappear, their places being taken by Armeria, Festuca, Erythrea, Juncus sp., &c.

The coast-flora of northern Europe contains few shrubby plants—the most important is Hippophae. Further south much of the coast vegetation is shrubby, *e.g.* on the flatter shores of the Mediterranean. The shrubs are mostly low-growing and much branched, with xerophytic characters. Further south still, in the tropics, many shrubs and trees grow upon the coast.

Of the various formations which grow upon tropical coasts the chief is the *mangrove-formation*, found covering the muddy swamps at the mouths of rivers and elsewhere, over which the tide flows daily, leaving the mud bare at low water. The plants found here present a great similarity in habit and other features, though belonging to different families. In the Old World about 22 species occur, in America four. The chief genus is Rhizophora ; Bruguiera (Rhizophoraceae), Avicennia (Verbenaceae), Aegiceras (Myrsin-

aceae), Sonneratia (Blattiaceae), and *Acanthus ilicifolius* are other important members of the group. In general these plants are much branched, with a great development of aerial roots, both 'flying-buttress' roots (p. 24) from the main stem and supporting 'pillar' roots (p. 24) from the branches. In Sonneratia, Avicennia, and Bruguiera, peculiar erect 'aerating' roots rise out of the mud (cf. Taxodium, Jussieua, &c.). These are covered with a loose, corky tissue (*aerenchyma*), formed by a phellogen, and containing large intercellular spaces. From them oxygen for respiration passes down to the other roots buried in the mud where there is none. The seeds of many mangroves germinate in the fruit (so-called *viviparous* germination) while still attached to the tree, and develope long radicles, which hang down, often to the length of a foot. When the seedling falls the root sticks into the mud, and thus the danger of being carried away by the tide is escaped. The mangroves are xerophytic in structure, with thick fleshy or leathery leaves, thick cuticle, water-tissue, &c.

In Asia and Australia there often occurs, further inland than the mangroves, a vegetation composed chiefly of the 'stemless' palm, *Nipa fruticans ;* in America a somewhat similar part is played by Bactris.

Another formation in the Old World is that characterised by Barringtonia sp., and others also occur (see Schimper and Warming, cited in Literature at end of chapter). Herbaceous shore-plants, *e.g.* Spinifex, many grasses, &c., are also common in the tropics.

On salt steppes and deserts other halophytes occur, *e.g.* the genera Haloxylon, Halimodendron, Anabasis, &c., together often with Salicornia, Suaeda, Atriplex, Sarcobatus, &c. All these exhibit characters like those of the sea-coast species.

Many shore plants in Europe are also found on mountains, a fact easily understood after a comparison of the general conditions of life, &c. Thus in Britain, Armeria, *Plantago maritima, Silene maritima, Cochlearia maritima,* &c., occur on the mountains at high levels as well as at the coast, but are rare or unknown in the intermediate districts, and in the same way, on the west coast of Scotland some alpine forms, *e.g. Saxifraga oppositifolia,* occur at the sea-side.

For further details of the structure and natural history of these Plants, see Pt. II., and Literature at end of chapter.

Alpine and Arctic Plants. We have pointed out above the resemblance between the flora of the higher parts of the mountains of the north temperate zone and that of the arctic regions ; this is specially well seen in the Grampians, to which we shall specially refer in this article. The general habit and structural features of alpine plants are much the same all over the world and resemble those of arctic plants.

In the arctic regions the conditions of life are peculiar ; the period of the year during which growth can take place is very short (1—4 months); the average temperature is low ; the light is bright and long-continued and the sun describes an almost complete circle every day, so that the light falls upon the plants from every side in turn at a comparatively low angle ; the soil is thin, and liable to be very much heated at the surface whilst it remains very cold at a little depth (thus hindering absorption by the roots) ; insects are few and far between, and belong chiefly to the lower classes (pp. 64, 103), especially the Diptera. It is evident therefore that xerophytic structure is a necessity, and in fact it is very marked in the arctic flora. The long-continued light retards growth and the plants show a dwarfed and tufted habit, as may be seen in the common genera Diapensia, Draba, Loiseleuria, Vaccinium, Saxifraga, &c. They also exhibit many of the xerophytic characters described above—reduced surface, closely-packed leaves, inrolled leaves, fleshiness, thick cuticle, hairiness, sunk stomata, and so on. The flowers show, as compared with the same species in warmer regions, an increased tendency to autogamy, and there is a marked increase of vegetative propagation, especially in species that are not capable of autogamy. Eutropous flowers are few, and often have shorter tubes, which enable hemitropous insects to reach the honey (p. 103). The genera above mentioned grow chiefly in the more rocky or dry places ; the wetter moors are occupied by such plants as Juncus, Scirpus, Carex, and many grasses. Most of these are characterised by erect (centric, p. 30) stems or leaves, so that the green tissue is

almost or quite symmetrically arranged, facing to every quarter of the compass. Jungner (see Literature) regards this as an adaptation to the peculiar 'circumpolar' light that falls on every side of the plant in turn. Annual plants are comparatively few in number, and few woody species occur; the arctic species of Betula, Salix, &c. are low-growing, almost herbaceous plants.

When we examine the flora of the Grampians or the mountains of Norway or Germany, its resemblance to that of the arctic regions is at once evident, most of the species being the same. At low levels the flora is like that of the lowlands from which the mountains rise, but marked by the absence of many species and the presence of others (sub-alpine), *e.g.* Meum, *Viola lutea*, &c. As we ascend, the lowland species gradually disappear; very few of them reach above 1000 feet in the Grampians, and these mostly do not pass above 3000 feet, while other species take their place and in turn disappear at still higher levels. The upper limit of trees (Coniferae and Betula) lies at about 2000 feet in the Grampians, but higher in more southern mountain ranges. The region between this limit and the snow-line is called the *alpine* region, and is inhabited by the more strictly alpine plants, which do not descend into the plains, though they often occur as sea-coast plants, or (in the tropics) as epiphytes (see p. 186).

The conditions of life in this region resemble those of the arctic regions sufficiently nearly to enable the same species to live in both. The air is moister in the alpine region, especially in the lower part, but the low barometric pressure favours transpiration; the light is more intense than at low levels, and on high plateaux is more or less circumpolar; the vegetative season is short; the soil is cold; there is much wind; the frequent presence of clouds diffuses the light and saturates the air at certain times.

The composition of the flora depends upon the soil and other conditions, though the plants themselves are all more or less xerophytic. Upon the high-level plateaux where the soil is cold and wet the dampest parts are occupied chiefly by peat-forming mosses, but on the firmer parts of the peaty soil occur species of Juncus, Eriophorum, Eleocharis, Carex, Scirpus, Festuca, Nardus, &c. All these show a

more or less centric or 'circumpolar-light' structure. Of the various climatic factors above mentioned, the circumpolar light is the most marked in such localities, and some authors regard the form of these plants as a direct result of its action; whether this be so or not they are well suited to make the best use of it. Most of them contain large airspaces, intercellular or enclosed by the leaves; these are sometimes regarded as protections against cold (see p. 172), the air they enclose being warmer than the outside air. On the summits of the ridges, where the soil is drier and more rocky, the vegetation consists largely of such plants as Calluna, Loiseleuria, Vaccinium, Arctostaphylos, Gnaphalium, Empetrum, Lycopodium, &c. All are pronounced xerophytes, usually evergreen, and thus the winter's cold becomes perhaps the most important factor in their life. Most of them have more or less inrolled leaves, which perhaps, as we have seen, act as a protection against the cold; at the same time these leaves have palisade tissue almost all round and stand more or less erect, so that they are well suited to the circumpolar light. Such leaves are termed by Jungner *cold-leaves.*

There is no perpetual snow in the Grampians, but heaps of snow lie until July or August in hollows on the mountains, and the plants growing near them are thus subjected in a more marked degree than elsewhere to a cold wet soil and atmosphere. In such places are found chiefly *Salix herbacea* and *reticulata, Oxyria digyna, Saxifraga stellaris, Vaccinium myrtillus,* &c. Most of these have thin deciduous leaves, round in shape, with serrated edges. These are termed *alpine snow-leaves* by Jungner; they are well able to survive burial in snow.

The open slopes, where the ground is not very wet, are chiefly covered by *Alchemilla alpina,* Erica, Calluna and Vaccinium, with patches of grasses, *Potentilla Tormentilla,* Polygala, Trientalis, and other flowers. The wet places by the sides of streams are occupied by mosses, liverworts, and a few flowering plants, *e.g.* Saxifraga sp. (especially *S. stellaris* and *aizoides*), Chrysosplenium, Caltha, Geranium, *Geum rivale,* &c. Many of these are lowland species which in sheltered glens ascend to great heights and mingle with the descending alpine forms.

Upon precipitous rocks a different flora appears. Here the soil is even more shallow than on the gentler slopes, and only those species with good tap-roots are usually able to live in such situations. The xerophytism is very marked, for the water supply is very limited. Here occur *Thalictrum alpinum, Silene acaulis, Arenaria Cherleria, Cerastium alpinum* (hairy), *Sedum rhodiola* (fleshy), *Saxifraga oppositifolia* (fleshy), Saussurea (hairy), Hieracium sp., Juniperus, and others. In wet places other forms occur, and many lowland species also, such as *Alchemilla vulgaris, Lychnis dioica,* Oxalis, *Lotus corniculatus,* &c.

All these alpine forms show more or less marked xerophytic characters—hairiness, fleshiness, reduction of surface, tufted and compacted growth, &c. On the Alps and on other mountains similar conditions of life occur at similar distances below the snow line, and the flora, though differing in composition, exhibits similar biological features. Details must be sought elsewhere.

Many plants which are characteristic of the shore-flora occur at high levels in the Grampians and other mountains, *e.g.* Armeria, Plantago sp., Cochlearia sp.; this has been explained above.

Lastly, we must briefly consider the question of reproduction. In the mountains of Britain and Norway insects are scarce at high levels, and are chiefly humble-bees and flies. Those flowers which like Vaccinium, Erica, Calluna, &c., or Alchemilla, Saxifraga, Potentilla, &c., are adapted to one or other of these groups, form the chief features of the entomophilous flora of these regions. Anemophilous flowers (*e.g.* Thalictrum, Cyperaceae, Juncaceae, Gramineae) are very abundant. Vegetative reproduction is common (specially interesting cases are *Polygonum viviparum, Saxifraga cernua,* &c.) and in general the floral features and mechanisms resemble those of the arctic regions. In the Alps it is different. At high levels butterflies and moths abound, and the flowers adapted to them figure largely in the flora, *e.g.* Gentiana, Viola, Silene, Dianthus, Daphne, Primula, &c. Insect visitors are present in sufficient numbers to enable most flowers to do without much self-fertilisation or vegetative reproduction. They have apparently determined the evolution of the endemic species into

butterfly-flowers, &c., for there are many cases where the alpine species of a genus belongs to class F, the lowland to classes with shorter tubes, *e.g.* H.

The flowers of alpine plants show, in general, brighter colours than those of low levels; this is apparently a direct effect of the brighter light.

For further details see Part II. and Literature.

Parasites.   These are plants which draw the whole or part of their food-materials from other plants by means of special organs termed *suckers* or *haustoria.*   They are very numerous among the Fungi, and there are many parasitic seed-plants, certain orders being entirely composed of them, *e.g.* Loranthaceae, Rafflesiaceae, &c.   In most of these cases the suckers are modified roots, developed from the parasite at points of close contact with the *host,* as the plant upon which it grows is termed.   The sucker penetrates the tissues of the host plant, probably by some kind of ferment-action, and grows into organic union with them; if the host grow in thickness, the suckers grow in length to keep pace with it. Some parasites are confined to one species of host, others are more general in their attacks.

Parasites are classed as *total* or *partial,* according to whether they take all or only some of their nourishment from the host.   In the latter case they appear only to take raw materials—the water and other substances absorbed by the roots—and therefore require green tissue of their own. In the former case chlorophyll is rendered useless, and they possess none; their leaves also are reduced to a more or less rudimentary condition (p. 30), or even the whole shoot, as in Rafflesiaceae, where the vegetative body is reduced to a mycelium like that of a fungus.   The inflorescence of parasites, on the other hand, is comparatively little degraded in structure.

The simplest form of partial parasitism is exhibited in the Rhinanthus group of Scrophulariaceae (*q.v.*), and in Thesium and some Santalaceae; all these are parasitic by their roots upon the roots of grasses, &c.   Viscum and other Loranthaceae, Myzodendraceae, &c., are parasitic upon the stems of their hosts, and are easily mistaken for epiphytes.

Total parasitism is well shown in Cuscuta and Cassytha,

with their twining stems and absence of chlorophyll and of leaves; these are both parasitic upon stems, while Orobanche, Lathraea, &c., are total parasites upon roots. A further step in the degradation of the vegetative system leads to the very remarkable orders Balanophoraceae, Hydnoracea, and Rafflesiaceae, above mentioned.

For further details see Pt. II. and Literature at end of chapter.

Saprophytes. These are plants which grow upon decaying organic matter and absorb the products of decay. The group includes most of the Fungi, perhaps a few Mosses, &c., and a few flowering plants, *e.g.* the Orchidaceae Neottia, Epipogon, and Corallorhiza, the Triuridaceae, the Burmanniaceae, and Bartonia, Monotropa, &c. The prothallus of Ophioglossum is also saprophytic.

It is probable that many plants are more or less saprophytes in a sense. The complete saprophytes above mentioned have no green tissue at all, for they take in their carbon from the soil in the form of complex organic compounds. These bodies possess potential energy, and therefore the absorption of light-energy becomes needless. Chlorophyll is thus rendered useless and is no longer produced, while at the same time, as there is no absorption of carbon dioxide from the air and the elaboration of new protoplasm may go on anywhere in the plant, the leaves, as in total parasites, are rendered useless also (being needed neither for assimilation nor transpiration), and are reduced to small scales. Many of these plants, *e.g.* Monotropa, possess a mycorhiza (p. 23), and it is very likely that all plants which have this *symbiosis* (or living together for mutual benefit) with the fungus are to some extent saprophytic, in that they take up more or less of the complex products of decay from the soil.

For further details see Pt. II. and Literature.

Insectivorous Plants. Under this title we have to consider a group of plants obtaining more or less nourishment from the dead bodies of small animals captured by means of special apparatus. There are about 400 species of these plants, belonging to 16 genera. The orders in which they occur are the Droseraceae (Drosera, Drosophyllum, Dionaea, Aldrovanda, &c.), Sarraceniaceae (Sarracenia,

Heliamphora, Darlingtonia), Nepenthaceae (Nepenthes), Cephalotaceae (Cephalotus), and Lentibulariaceae (Pinguicula, Utricularia, Genlisea, &c.). Of these the genera Drosera, Pinguicula and Utricularia occur in Britain.

Insectivorous plants may be divided into groups according to their mode of catching their prey. In the first group—those with glandular hairs secreting a sticky fluid to which insects, mistaking it for honey, adhere—are placed Drosophyllum, Byblis, Roridula, Pinguicula, Drosera. In the two last-named movements of the leaf or tentacles occur when stimulated by the presence of proteid bodies. All these plants secrete a digestive fluid which dissolves the greater part of the animal substance. In the second group—plants with sensitive motile organs, which close upon the prey—are placed Dionaea and Aldrovanda, in both of which part of the leaf is modified to form the trap. Digestive fluids are secreted in these also. A third group is formed by the pitcher plants—Nepenthes, Cephalotus and the Sarraceniaceae—in which the leaves or portions of them form upright pitchers with hoods over their mouths. The upper part of the pitcher secretes honey, which attracts flies, and these gradually get further into the pitcher ; the inner surface is slippery and they find it more easy to go downwards than to return and are ultimately drowned in the water at the bottom. It is doubtful whether the plant in these cases secretes a digestive ferment, or whether it merely absorbs the products of decay and is thus saprophytic; the water in the pitcher swarms with bacteria, which rapidly decompose organic matter. Lastly there is the group of ‘eel-trap’ plants—Utricularia, Biovularia, Polypompholyx and Genlisea—in which animals are caught in traps of various shapes, from which there is no escape. They decay and the plant absorbs the products.

Full details of these plants will be found in Pt. II. ; see also the Literature at the end of the chapter.

Zones of Vegetation. The local distribution and the periodicity of the climatal factors—light, heat, and moisture—are accompanied by a corresponding division of the earth's surface into *zones of vegetation*, *i.e.* zones occupied by similar forms of vegetation, with the same periods of growth and with similar adaptations to their environment.

These divisions are purely biological, and in dealing with them the systematic relationships of the plants are neglected. Drude enumerates six of these zones (see Map III. of his Atlas), as follows.

I. *Northern glacial zone.* This consists of the arctic region (including the Tundras), and is limited on the south by the northern limit of trees (*i.e.* the limit beyond which they do not naturally occur). The period of growth and vegetation lasts about three months, reaching its maximum in July. A corresponding region, counted as part of this zone, occurs above 15,000 feet in Thibet and in other northern mountain regions. Large areas are covered by mosses and lichens; others by perennial herbs and undershrubs, of xerophytic character (see above).

II. *Northern zone of cold winters.* This extends from the northern limit of trees to the latitude in which evergreen branched trees and shrubs begin to predominate, and in which the country is parched in summer. It reaches in Europe to the south of France and to Greece, and in Asia to about 50° N.; in North America it includes most of Canada, the western United States as far south as Utah, and the New England States. Corresponding areas occur in the various mountain-ranges. The period of vegetation lasts during 3 to 7 months, with its maximum in July; the summers are not so dry as to parch the vegetation. Extensive areas are covered with masses of vegetation of similar aspect; such may be termed *plant-formations*, a term of somewhat wider scope than forms of vegetation. The chief formation is that of the forests, which occupy vast areas in this zone, though much reduced by man's operations in modern times. The chief elements are the Conifers (Abies, Pinus, Larix, &c.), mostly with evergreen xerophytic leaves (Larix, the most northern form, is deciduous), the catkinate families (Fagaceae, Betulaceae), Acer, Tilia, Fraxinus, &c. Many of these form homogeneous forests, of one species only, in certain regions, *e.g.* pine, birch, beech, &c. All but the Conifers are deciduous. The undergrowth of such forests consists of young trees of the same species, and of a few shrubs and small woody climbers (*e.g.* Lonicera); on the soil grow ferns (never arborescent), grasses, and various herbs. The latter are characterised by their early develop-

ment in spring, before the trees are in full leaf, so that they obtain the maximum of available light. Familiar instances are the primrose, violet, hyacinth (Scilla), Adoxa, Anemone, &c. Later in the year the saprophytic plants (Monotropa, Neottia, &c.) appear. Epiphytic phanerogams do not occur, but in very moist places ferns are often epiphytic, and the tree-bark is usually covered with algae, lichens, liverworts, &c. Another formation is that of copses of small trees and larger shrubs, such as willow (Salix), hazel (Corylus), hawthorn (Crataegus), &c. Another is that of the heaths, which cover immense areas in some parts of this zone. The chief plants of this formation are the Ericaceae, Calluna, Erica, and Vaccinium; others are gorse (Ulex), Ledum, Salix sp., &c.; among these occur grasses and other herbaceous plants. Lastly, there are the grass-formations, in which the Gramineae (or in wet ground the Cyperaceae) dominate, forming a turf; amongst them grow numerous herbaceous plants, *e.g.* many Compositae, Campanulaceae, Labiatae, Scrophulariaceae, Umbelliferae, Onagraceae, Leguminosae, Geraniaceae, Cruciferae, Caryophyllaceae, Ranunculaceae, Polygonaceae, Liliaceae, Juncaceae, &c. In the more southern parts of this zone rain is rare in summer, and the transition to the following zone is gradual.

III. *Northern zone of hot summers.* This comprises the subtropical regions lying between zones II. and IV., *i.e.* the basin of the Mediterranean (including Spain and Italy), Asia south of zone II. (excepting India, Indo-China, the Malay Archipelago, and the S.E. coast of Arabia), North Africa, the Sahara, and the rest of the United States and Mexico. The summer temperatures are very high, higher than in the tropics; at night it is often cold. There is no real winter, but at most a slight interruption of vegetation in January. The vegetation is chiefly xerophytic. Coniferae with needle-leaves appear in large numbers in the forests; most of the trees and shrubs are evergreen and with branched stems, but there are a number of deciduous forms which bear their leaves in the wet season. Epiphytic ferns occur in the wetter regions. Copse-formations are frequent, *e.g.* the 'maquis' of the Mediterranean coast (Myrtus, Laurus, Olea, Buxus, &c.), the 'chapparal' of Mexico, Texas, &c. (Adenostoma, Prosopis, &c.), the Larrea scrub, &c. The

grass-formations (steppes and prairies) are parched in summer. The driest regions of this zone, *e.g.* the Sahara, parts of Mexico, &c., are occupied by succulents or other extremely xerophytic plants.

IV. *Tropical zone.* This includes most of the land between the Tropics, where the rainfall is sufficient to prevent the formation of deserts. There is no interruption of the period of vegetation by cold, but in all the continental parts, excepting western equatorial Africa, the extreme south of India, the Amazon valley, the extreme north of Australia, &c., there is a dry season of at least three months, interrupting vegetation and necessitating a xerophytic character in the plants. In the areas just mentioned and in the islands (*e.g.* southern Ceylon, the Malay Archipelago, &c.), there is rain at almost all periods of the year and especially at the two seasons when the sun is vertically overhead. Here tropical vegetation is seen in its highest development. The bulk of the lowland area is (or was formerly) covered with dense forest. The trees composing the forests are of many species, and are very rarely of social habit; they are mostly evergreen and have either simple or branched stems. The simple-stemmed evergreens are characteristic of these regions; they are chiefly Monocotyledons, *e.g.* Palms, Pandanaceae, Musaceae, Bamboos, &c. The trees mostly have straight trunks reaching to a height of 50—100 feet or more and bearing their leaves and branches (if any) at the top, where they are exposed to the full sunlight. Buttress-roots (p. 23) are very often found at the base of the trunk. The leaves are mostly more or less leathery with thick cuticle (the characteristic sharp rattle of the rain-drops in a tropical forest is due to this, and also the brightness of the light reflected from the leaves); they are often corrugated (*e.g.* in Palms) or turned partly edgewise, or they stand with an upward slope, or (as in some Leguminosae) move upwards as the light becomes more intense, so that they obtain some protection against the radiation. The young leaves in some plants are produced at all periods of the year, in others periodically (often this periodicity has no direct relation to that of the climate); they have usually good arrangements for their protection in the bud (p. 168), and are very often red in colour. Those trees which have

not glossy leaves have usually rain-leaves (p. 154) with drip-tips. The air is almost always very moist, and transpiration is perhaps slower than in Europe (this is a disputed point at present). The flowers and fruits are very often borne on the older branches or even on the main trunk (p. 35); the reason for this is not known. Almost nothing is known of the relations of flowers and insects in the tropics. Many flowers are adapted to sun- or humming-birds (p. 103).

Below the larger trees are the shade-loving trees, whose crowns reach a height of about 30—50 feet, and below these again occur large herbs and undershrubs, whilst on the ground are mosses, Selaginellas, saprophytes, &c. Besides these, two forms of vegetation especially characterise the tropical forest—lianes and epiphytes, both of which occur in profusion in every available space, so that the forest as a whole forms an inextricable tangle of the most varied vegetation. Parasites are abundant, and myrmecophilous plants (p. 117) and other interesting forms are often found.

In those regions where there is a dry season of three months or more the flora has a xerophytic character, and a number of the forest trees have deciduous leaves (*e.g.* in the Catinga forests of Brazil); lianes are less common, epiphytes are few and of the most xerophytic kind (p. 186). Cacti, Euphorbias and other large xerophytic forms appear in large numbers, and with a few Acacias, &c., may represent the 'copse-vegetation' of the zone. Large open areas (savannahs) are covered with grasses (Chlorideae, Festuceae, &c.), Cyperaceae, Leguminosae, Myrtaceae, Rubiaceae, &c. In these savannahs the open 'grass' is often interrupted by forest or copse-wood areas.

V. *Southern temperate zone with hot summers.* This includes all the land south of zone IV., except southern Patagonia (and a corresponding belt in the Andes), Kerguelen Island, a belt in the mountains of Tasmania and New Zealand, and the antarctic lands and islands. The vegetative period is interrupted by more or less of winter about July, and in the northern parts there is more or less drought in summer. In Valdivia, Victoria, Tasmania and part of New Zealand, where there is plenty of rain at all times of the year, there are forests of evergreen and deciduous trees with many Conifers. In Paraguay, Natal

and eastern Australia the forests contain few Conifers; the evergreen trees are mostly much branched. Other areas, *e.g.* in Chili, S.E. Cape Colony, and parts of Australia, are covered by a 'scrub' or 'bush' of evergreen shrubs and small trees, usually of pronounced xerophytic character. The Pampas, the Kalahari desert and much of Australia, are covered with a turf of grasses and other xerophytic herbs, which becomes very parched in the dry season.

VI. *Southern cold zone.* This includes the areas mentioned by name at the beginning of the last paragraph. The vegetation is like that of zone I.—undershrubs, herbs, mosses, lichens, &c.

Floral Regions. In the earlier periods of the earth's history the climatic conditions appear to have been very uniform, and the various plants that then existed appear to have had almost universal distribution. This was facilitated by their spores being light and easily carried by wind to great distances (the Cryptogams are the most widely distributed of existing species). Towards the end of the secondary period the boundaries between the different regions of the earth appear to have become more clearly marked, and with them the climatic differences. At the same time the seed-plants, with their less perfect means of dispersal, arose, and the flora of the different regions thus became gradually different, the new plants evolved in various districts being checked in their spread over the globe by the various agents discussed above. This process continuing, it has gradually come about that at present the floras of different regions of the earth's surface differ very much in their composition, though they may agree in their general biological characters; the latter, as we have seen, are correlated with the climatal conditions, whilst the composition of the flora is often quite different in regions of similar climate and soil. Thus we are able to divide the earth's surface into a number of *floral regions*, taking no account of biological characters but only of the relationships of the plants. It is evident from what has been said that a floral region will be characterised by the possession of endemic forms; the greater the number of these and the higher their systematic rank the more natural is the region. Most of the natural orders have a very extensive distribution, and occur in many of the floral regions;

the possession of many endemic genera, tribes and sub-orders, more or less closely allied, is regarded as sufficient to mark a floral region. The various regions graduate into one another at their edges, and isolated districts belonging to one region often occur in the midst of another (*e.g.* on the mountains). It is found that the different regions may be grouped into three chief divisions, the *boreal* or northern extra-tropical, the *tropical*, and the *austral* or southern extra-tropical. The number and extent of the floral regions of the globe is differently estimated by different writers; we shall follow here the arrangement given by Drude in his *Atlas der Pflanzenverbreitung* (see Literature at end of chapter). Space will only permit of an enumeration of the regions, with their chief characters (abridged from Drude). Each is again subdivided into *domains*.

I. Boreal Group. 1. *The Northern Floral Region.* This corresponds very closely to the first and second zones described above. The general systematic features of the flora resemble those of the British flora.

2. *The Central Asiatic Region.* This includes Turk-estan, Mongolia, and Thibet. The district is very dry in summer and there is much salt in the soil in many parts. Trees are very rare. Halophytes, *e.g.* many Chenopodiaceae, are numerous; other characteristic forms are shrubby species of Astragalus, Plumbaginaceae, &c.

3. *The Mediterranean and Orient Region.* This includes Spain, southern France, Italy, Greece, Asia Minor, Persia, the Punjab, and Africa and Arabia north of 24° N., together with the Canaries, Azores, &c. It is very closely allied to the preceding region, and possesses a very similar vegetation. A few palms occur here, *e.g.* Chamaerops and the date-palm (Phoenix). There are many Cruciferae, Umbelliferae, Tamaricaceae, &c., in this region.

4. *The Eastern Asiatic Region.* This includes the rest of China, with Corea and Japan, and possesses many endemic forms, *e.g.* the Conifers Cryptomeria, Ginkgo, Biota, &c., many Araliaceae, Lardizabalaceae, Menispermaceae, Magnoliaceae, Sapotaceae, &c.

5. *The Central North-American Region.* This is the region lying between region 1 and the tropical regions of Mexico and the West Indies; it includes the United States

with the exception of a part of New England, Washington State and Oregon, and includes also a portion of Canada as far as the Saskatchewan. The climatal conditions resemble those of the preceding regions. The flora includes many Compositae, Hydrophyllaceae, Polemoniaceae, Nyctaginaceae, Chenopodiaceae, Polygonaceae (§ Eriogoneae), &c.

II. Tropical Group. 6. *The Tropical African Region.* This includes all Africa and Arabia south of region 3, except the Cape-Colony region, and the islands on the east side. Palms, Pandanaceae, &c., are common in this region ; other characteristic plants are Adansonia, Salvadoraceae, &c. In the Kalahari desert occur Welwitschia, Acanthosicyos, and other peculiar forms.

7. *The East African Island Region.* To this belong Madagascar, Mauritius, the Seychelles, Mascarenes, &c. The flora shows relationships to those of both India and Africa. Many endemic forms occur, *e.g.* Lodoicea, Brexia, Chlaenaceae, &c.

8. *The Indo-Malayan Region.* This includes India, Ceylon, Burmah, Cochin-China, and the islands from Formosa to New Guinea, Polynesia, and northern Australia. Palms, Pandanaceae, Zingiberaceae, Musaceae, Pedaliaceae, Moraceae, Dipterocarpaceae, Nepenthes, and other forms abound in this region.

9. *The Tropical American Region.* Beginning in Florida and Central Mexico, this extends over the West Indies, Central America, the Amazon valley, Paraguay, Uruguay, &c. Characteristic plants are the Cactaceae, Loasaceae, Cyclanthaceae, Bromeliaceae, Velloziaceae, certain Palms, Marcgraviaceae, Vochysiaceae, &c.

III. Austral Group. 10. *The South African Region.* Though small, including only the area south of the Orange River, this region is wonderfully rich in endemic forms and contains a vast number of species. Among the characteristic forms are many Iridaceae, Amaryllidaceae, Liliaceae, Juncaceae (including Prionium), Restiaceae, Ericaceae, Bruniaceae, Penaeaceae, Proteaceae (chiefly Protea and Leucadendron), Selagineae (Scrophulariaceae), Diosmeae (Rutaceae), Acacias, Mesembryanthemum, Helichrysum, Pelargonium, Oxalis, Crassula, and many more.

11. *The Australian Region.* This includes Australia

(except the northern part belonging to region 8) and Tasmania. Haemodoraceae, Candolleaceae, Goodeniaceae, Epacridaceae, &c., are endemic. Besides these there are many representative forms of Restiaceae, Xyridaceae, Juncaceae, Liliaceae (Xanthorrhea, &c.), Myoporaceae, Myrtaceae (Eucalyptus, &c.), Proteaceae (Banksia, Hakea, Grevillea, &c.), Acacia, Pimelea, Casuarina, Callitris, &c.

12. *The New Zealand Region.* Though so near to Australia, New Zealand shows more relationship in its flora to the Andine region. The flora is very peculiar, and appears to have been derived from all the surrounding regions. Tree ferns form a large part of the vegetation.

13. *The Andine Region.* This includes South America south of the Rio de la Plata (except the portion in region 14) and Paraguay together with the Andes and the coasts of Chili and Peru. There are many shrubby Compositae, also Calyceraceae, Plumbaginaceae, Nolanaceae, Solanaceae, Scrophulariaceae, Escallonias, Tropaeolaceae, Oxalis, &c.

14. *The Antarctic Region.* This corresponds to the sixth zone of vegetation described above. There are many characteristic Gramineae, Juncaceae, Umbelliferae, &c., and such genera as Bolax, Pringlea, Acaena, &c.

Advanced students should consult various books and papers dealing with the subjects of this chapter. Among these may be mentioned the following. *Geographical Distribution* &c. Drude's *Handbuch der Pflanzengeographie* or the French translation by Poirault; his article in Schenk's *Handbuch der Botanik*, vol. III. and his *Atlas der Pflanzenverbreitung*; Warming's *Oekologische Pflanzengeographie* (translated into German by Knoblauch); Engler's *Versuch einer Entwicklungsgeschichte der Pflanzenwelt*; Darwin's *Origin of Species*, &c.

General Natural History. A very good index to the Literature will be found in Warming's book (see above); see also Ludwig's *Biologie der Pflanzen*, Kerner's *Natural History of Plants* (Oliver's translation), Haberlandt's *Botanische Tropenreise*, Wallace's *Tropical Nature*, &c.

Water-plants. Schenk, *Die Wassergewächse* (Bonn 1886), and *Anatomie d. submersen Gewächse* (Bibliotheca Botanica); Goebel's *Pflanzenbiologische Schilderungen*; Staes in *Bot. Jaarboek*, Gent, 1889, &c.

Climbing Plants. Darwin's *Climbing Plants*; Schenk's *Biologie und Anatomie der Lianen* (Jena 1892); physiological text-books, &c.

Xerophytes. Ludwig, Warming, Goebel, and Kerner, *op. cit.*; Volkens' *Flora d. aegyptisch-arabische Wüste*, and many papers (see Warming).

Epiphytes. Schimper's *Epiphytische Vegetation Amerikas* (Jena 1888); Goebel *op. cit.*; Willis and Burkill's *Flora of Pollard Willows* in *Proc. Camb. Phil. Soc.* 1893; Groom in *Nat. Science* 1893, &c.

Halophytes &c. Warming and Goebel *op. cit.*; Schimper's *Indo-malayische Strandflora* (Jena 1890); and papers quoted in Warming.

Alpine and Arctic Plants. Müller's *Alpenblumen*; Warming *op. cit.* (see literature there quoted); Jungner, *Klima und Blatt in der Regio alpina*, Flora 1894.

Parasites and Saprophytes. Warming, Kerner, Ludwig, *op. cit.*; Hemsley in *Linn. Soc. Journ.* XXXI.; papers by Groom in *Annals of Bot.*, recent years.

Insectivorous Plants. Darwin's *Insectivorous Plants*; Goebel *op. cit.*

Miscellaneous (bud protection &c.). Potter in *Linn. Soc. Journ.* 1888, Keeble in *Annals of Bot.* 1895, Stahl in *Ann. Jard. bot. Buitenzorg* 1893, Groom in *Linn. Soc. Trans.* 1893.

Other papers are mentioned in the text, and references will be found in many of the books above quoted.

CHAPTER IV.

ECONOMIC BOTANY.

ECONOMIC botany is the study of plants from the point of view of their immediate practical uses in yielding foods, building materials or other useful products. We know that the botanical characters of the plants of any one family are very similar, and this principle may be applied to economic botany also; if a given species is useful for some character it possesses, its near relatives are more likely to resemble it in this than comparatively unrelated forms. Space will not permit of more than a brief enumeration of some of the most important classes of economic products, with the chief plants from which they are obtained. No mention is made of Bryo- or Thallophytes.

Metabolism. In a green plant the roots absorb water and other substances from the soil, and the leaves obtain carbon from the air. Assimilation (p. 25) goes on in the leaves and new protoplasm is made, which as fast as it is formed decomposes into simpler substances, chiefly sugar and amides, which are carried away by the phloem to those parts of the plant where they are required. This continual chemical change which is going on is termed *metabolism*, and may be divided into *anabolism*, the building up, and *katabolism*, the breaking down, of complex materials. The materials carried away in the phloem are either used at once at the growing parts or as food by the living cells, or else they are stored up as *reserves* for future use. All seeds contain reserves and so do all plants which die down at any period of the year or are arrested in their growth by cold or drought. Reserves are also made in many cases

(Agave, many Palms, &c.) to enable the plant to produce a great mass of flowers and seeds at some future time.

In plants which are not green (saprophytes and parasites), all the food is taken from the soil or from the host and the metabolism is correspondingly altered in detail.

No accumulation of the products of the different steps in anabolism takes place, the upward progress to protoplasm being gone through very rapidly, but with katabolism it is different and accumulations of the products occur; it is with these we have now chiefly to deal. The first downward step is the decomposition of protoplasm into *proteids* (complex organic bodies containing carbon, hydrogen, oxygen, and nitrogen); the next is to *amides* (crystallisable organic bodies, containing the same elements; the commonest is asparagin); then, by elimination of nitrogen, the *carbohydrates* (bodies containing carbon, hydrogen and oxygen in the proportions $C_xH_{2y}O_y$; the chief are starch, cane-sugar, grape-sugar or glucose, mannite, inulin, and cellulose), the *oils* or fats (containing C, H, O), and other bodies, are formed. A further decomposition may take place, in respiration (which is the expression of katabolism), giving as final products carbon dioxide and water. All the products mentioned so far are capable of being used again in the metabolism of the plant, but there are others which are apparently waste-products. Only rarely are these excreted at the surface; usually they are stored in the cells or in special cavities or passages. Some of these bodies are of economic value, *e.g.* resins, alkaloids, ethereal oils, wax, &c.

In forming reserves the plant always stores up both nitrogenous and non-nitrogenous materials. The former take the shape of proteids in seeds; in other places they may be proteids or amides. The latter in seeds are usually stored as starch or cellulose (*starchy* seeds) or as oils (*oily* seeds); in other places other forms occur. In germination ferment-action causes the decomposition of the reserves and their transmutation to sugar and amides, in which forms they travel through the plant.

We shall now deal briefly with the chief classes of economic products, and enumerate the principal genera of plants that supply them. Details will be found in Pt. II.

For any single product whose source is required reference should be made to the index.

Food of Man.　Animals require proteid materials in their food.　Protoplasm occurs of course in all living parts of plants, but is usually enclosed in a disproportionate mass of cellulose, &c.　The staple food-stuffs are obtained from those parts in which the plant has made reserve-stores, *e.g.* seeds, tubers, bulbs, &c.　The most important food-stuffs are the fruits of the cereal grasses, whose seeds have a starchy endosperm (flour), *e.g.* rice (Oryza), wheat (Triticum), oats (Avena), rye (Secale), barley (Hordeum), and maize (Zea), to which may be added Euchlaena, Sorghum, Coix, Setaria, Panicum, Zizania, and others.　The seeds of buck-wheat (Fagopyrum), and of pea (Pisum), bean (Vicia), lentil (Ervum), chick-pea (Cicer), dhal (Cajanus), Arachis, Voand-zeia, Dolichos and other Leguminosae are also valuable food-stuffs, as well as those of coco-nut (Cocos), chestnut (Castanea), walnut (Juglans), hickory (Carya), Caryocar, Brosimum, Bertholletia, Lecythis, Telfairia, Pistachia, Cas-tanospermum, Corylus, Nelumbium, Trapa, Dioon, Arau-caria, &c.

Many fleshy fruits form valuable food-stuffs.　The most important is the banana (Musa) with its ally the plantain; these form a great part of the food of a large proportion of the world's inhabitants.　Other very important fruits are the date (Phoenix), bread-fruit and jack (Artocarpus), mango (Mangifera), fig (Ficus), orange, lemon, &c. (Citrus), pear, apple, &c. (Pyrus), grape (Vitis), pine-apple (Ananas), pomegranate (Punica), plum, apricot, cherry, &c. (Prunus), papaw (Carica), custard-apple (Anona), bramble or black-berry, raspberry, &c. (Rubus), gooseberry, currant, &c. (Ribes), strawberry (Fragaria), &c.　To these may be added a long list of fruits, chiefly tropical, belonging to the genera Aberia, Achras, Averrhoa, Anacardium, Anona, Artabotrys, Bactris, Benincasa, Blighea, Borassus, Byrsonima, Celtis, Cereus, Chrysobalanus, Chrysophyllum, Citrullus, Coccinia, Coccoloba, Cucurbita, Cucumis, Cydonia, Debregeasia, Decaisnea, Dialium, Diospyros, Durio, Eriobotrya, Eugenia, Feronia, Garcinia, Gaylussacia, Glycosmis, Hymenaea, Juni-perus, Lapageria, Lantana, Litchi, Macadamia, Maclura, Mammea, Mimusops, Monstera, Morus, Myrtus, Nephelium,

Opuntia, Osmanthus, Pappea, Passiflora, Pereskia, Persea, Peumus, Phaseolus, Prosopis, Psidium, Sechium, Spondias, Tamarindus, Vaccinium, Vitellaria, Zanthoxylum, Zizyphus, and many others.

Underground reserve-stores are also an important source of food. The chief are perhaps the tubers of potato (Solanum) and yam (Dioscorea), the rhizomes of arrowroot (Maranta) and taro or tania (Colocasia), the roots of cassava or tapioca (Manihot), sweet potato (Ipomœa), turnip (Brassica), beetroot (Beta), &c., the bulbs of onion, garlic, &c. (Allium), and others. To these may be added the genera Arum, Canna, Commelina, Daucus, Helianthus, Oxalis, Peucedanum, Pachyrrhizus, Priva, Raphanus, Scilla, Scorzonera, Sechium, Selinum, Stachys, Tragopogon, Tropaeolum, Ullucus, Xanthosoma, and others. There are numerous plants with small tubers or other underground parts which might be improved by cultivation, and that deserve trial.

Trees and shrubs, as we have seen, usually store reserves in their woody stems. Food-products are obtained from the stems of sago (Metroxylon) and other palms (*e.g.* Caryota, Arenga, &c.), Cycas, Alsophila, Acer (sugar), &c.

The leaves of cabbage and its varieties (Brassica) and the inflorescences of cauliflower (Brassica) contain reserves and are used as food. The leaves of many plants are eaten, but are not of much food value; such are lettuce (Lactuca), celery (Apium), sea-kale (Crambe), cress (Lepidium), rhubarb (Rheum), spinach (Spinacia), Ceratopteris, Chenopodium, Eremurus, Foeniculum, Myrrhis, Scorzonera, Tetragonia, and others. The young bud of leaves in some palms is eaten as 'cabbage,' *e.g.* Oreodoxa, Cocos, &c.; the young flower-heads of Cynara (artichokes) are also valuable as a vegetable; to these may be added the young shoots of Asparagus and Bambusa.

Several of the last-mentioned products are rather *condiments* than food. To them may be added many more, *e.g.* mustard (seed of Brassica), capers (buds of Capparis), cayenne pepper (Capsicum), caraway (Carum), cinnamon (Cinnamomum), horse-radish (Cochlearia), cloves (Eugenia), cress (Lepidium), nutmeg (Myristica), water-cress (Nasturtium), dill (Peucedanum), anise (Pimpinella), pepper (Piper), vanilla (Vanilla), ginger (Zingiber), Allium, Archangelica,

Carum, Coriandrum, Crithmum, Cucumis, Cuminum, Illicium, Mentha, Monarda, Monodora, Myrrhis, Ocimum, Olea, Origanum, Pimenta, Salvia, Satureia, Smyrnium, Tropaeolum, Thymus, &c.

Many drinks are prepared from plants. Intoxicating liquors are generally prepared by fermentation of liquids containing sugar. We have seen that the non-nitrogenous reserve-materials are usually carried about in the form of sugar. When such a plant as Agave, or one of the palms which only flowers once, is producing its inflorescence there is a great rush of sugar upwards in the stem, and this may be tapped and fermented; see Agave, Borassus, Cocos, &c. Other drinks are prepared by fermenting the sugar derived from the starch of seeds in germination, *e.g.* sprouting barley, &c. Infusion-drinks are prepared from coffee-seeds (Coffea), cocoa (Theobroma), tea (Thea), maté (Ilex), Cichorium, Cola, Catha, Priva, Stachytarpheta, &c. The milk of young nuts of Cocos is a useful beverage in the tropics. A milk (latex) is also obtained from Brosimum, Mimusops, &c.

Stimulants and narcotics are obtained from hemp (Cannabis), opium (Papaver), tobacco (Nicotiana), Erythroxylon, Cola, Areca, and other plants.

For other food-stuffs, and for individual products, see the General Index (Vol. II.), *e.g.* under Sugar, Manna, &c., and see below under Oils.

Food for Domestic Animals. This may be divided into (i) plants used for direct grazing, and (ii) food products prepared from plants for subsequent use, as hay, roots, &c.

Pasture, &c. The Gramineae form the staple food of grazing animals. There are many useful grasses, varying according to the climate; *e.g.* Agrostis, Alopecurus, Andropogon, Anthoxanthum, Aristida, Avena, Bouteloua, Briza, Bromus, Chionachne, Chloris, Cynodon, Cynosurus, Dactylis, Deschampsia, Eriochloa, Festuca, Holcus, Hordeum, Lolium, Melica, Milium, Panicum, Phleum, Poa, Secale, Tripsacum, Trisetum, Triticum, &c. Other useful plants are clover (Trifolium) and other Leguminosae, *e.g.* sainfoin (Onobrychis), vetch (Lathyrus and Vicia), lucerne and medick (Medicago), Acacia, Anthyllis, Astragalus, Ervum, Hippocrepis, Lotus, Lupinus, &c. To these may be added comfrey (Symphytum), spurrey (Spergula) and many other plants.

Fodder, &c. Most of the above plants are equally valuable in hay. Cattle are also fed on many of the plants used for human food, *e.g.* turnips, beans, &c., on the pods of several Leguminosae, *e.g.* Ceratonia, Cicer, &c., the fruits of Argania, and other products.

Silkworms are reared on the leaves of mulberry (Morus), and also on those of Ailanthus, Maclura, &c.

Many plants are useful for providing honey and pollen to bees; those belonging to classes H, B′ and B, whose flowers have tubes of not more than 6 mm. in length, are best for this purpose, this being the length of a hive-bee's tongue. Among the best are Acer, Borago, Brassica, Calluna, Echium, Erica, Eucalyptus, Fagopyrum, Gossypium, Helianthus, Lupinus, Medicago, Melilotus, Mentha, Nepeta, Origanum, Onobrychis, Prunus, Pyrus, Reseda, Ribes, Rosa, Rubus, Salix, Salvia, Thymus, Tilia, Trifolium, Vaccinium, Vicia, Viola, &c. Care has to be taken to avoid plants such as Aconitum, with poisonous honey.

Timber. Ferns and Monocotyledons, with their scattered vascular bundles and usual absence of any regular growth in thickness, do not yield much useful wood, or at any rate not such as can be sawn into planks. The entire stems of bamboos, palms, &c., are largely used in building, and split portions are useful in roofing, &c. The most generally useful timber-plants are the Conifers, their wood being soft and the stems very straight; the resin prevents decay. The chief genera are Abies, Pinus, Sequoia, Larix, Cedrus, Chamaecyparis, Agathis, Taxus, Picea, &c. Other important timber-trees are Acer, Albizzia, Ailanthus, Betula, Brya, Bucklandia, Buxus, Caraipa, Casuarina, Carpinus, Carya, Castanea, Catalpa, Cedrela, Celtis, Chloroxylon, Corylus, Curtisia, Dalbergia, Diospyros, Duguetia, Eucalyptus, Fagus, Flindersia, Gleditschia, Gmelina, Grevillea, Guaiacum, Hymenaea, Juglans, Liriodendron, Metrosideros, Mesua, Ocotea, Ostrya, Platanus, Populus, Pterocarpus, Quercus, Rhus, Robinia, Salix, Sambucus, Santalum, Schleichera, Shorea, Swietenia, Tectona, Tilia, Tristania, Ulmus, Xylia, Zelkova, &c.

Fibre. Many plants yield valuable fibre, used for making cord, rope, &c. Fibres are the mechanical tissue of the plant (p. 26) and are arranged at the places where the strains occur. The amount of mechanical tissue developed

depends to a considerable extent upon the strain to which the parts are subjected, increasing with increase of strain. Other things being equal a plant living in a windy place has more fibre than one living in a calm place. In practice only herbaceous plants are used, on account of the difficulty of preparing the fibre; the commonest method is by maceration in water. The chief fibres thus prepared are flax (Linum), hemp (Cannabis), jute (Corchorus), sunn-hemp (Crotalaria), rhea (Boehmeria), New Zealand flax (Phormium), &c. To these may be added Agave, Fourcroya, Maoutia, Musa, Sanseviera, and others. Many palms have long fibres on the bases of the leaves; these are made up of many simple fibres united together, and are useful in rope-making and for many other purposes. Such are Arenga, Attalea, Borassus, Caryota, Cocos, Copernicia, Leopoldinia, &c. The leaves of some desert grasses are also used as fibres, *e.g.* Stipa (esparto), Lygeum, Ampelodesma.

The hairs upon the seeds or fruits of many plants are often long but rarely of much strength or flexibility. The only one of much value is the cotton (Gossypium).

Drugs. Innumerable plants are or have been used in medicine. No attempt has been made to mention all these cases nor even all the plants now used. Among those described in Part II. are Aloe, Alstonia, Amomum, Anamirta, Aralia, Atropa, Cannabis, Cascarilla, Cassia, Cinchona, Cinnamomum, Citrullus, Coix, Cola, Colchicum, Colutea, Digitalis, Dorema, Drimys, Elettaria, Erythroxylon, Ferula, Gentiana, Glycyrrhiza, Ipomœa, Lewisia, Lindera, Menyanthes, Papaver, Peucedanum, Pilocarpus, Pringlea, Rhamnus, Ricinus, Ruta, Santolina, Schoenocaulon, Smilax, Strophanthus, Strychnos, Tamarindus, Toluifera, Trigonella, Uragoga, Urginea, Veratrum, Verbascum, &c.

Gums, Balsams, Resins, Rubber, &c. Most of these substances appear to be waste-products as far as the plant itself is concerned, though they often have an incidental value, *e.g.* resins preserve wood from decay. Only rarely does the plant excrete these substances upon the surface; usually they are stored in laticiferous vessels, resin-passages or other receptacles, and only escape if these be cut into. Only a few of the principal products are mentioned here; for others reference must be made to the index (Vol. II.).

Camphor. This is obtained from Cinnamomum and Dryobalanops.

Caoutchouc, Gutta-percha, and *Indian rubber* are obtained from Bassia, Castilloa, Ficus, Hancornia, Hevea, Landolphia, Manihot, Mimusops, Palaquium, Payena.

Gums. Gum-arabic (Acacia), gum-tragacanth (Astragalus), gum-benzoin (Styrax) are all important products. Many trees yield gums, *e.g.* cherry. Other gum-yielding plants are Boswellia, Feronia, Opopanax, Prosopis, &c. It is hard to draw the line between some of these products and resins.

Resins, &c. These are chiefly obtained from Coniferae, Burseraceae, &c. The chief genera (*q.v.*) yielding resins (including under this heading such bodies as balsams, frankincense, guaiacum, &c.) are Agathis (dammar, kauri), Araucaria, Boswellia (frankincense, olibanum), Bursera, Callitris, Calophyllum, Canarium, Caraipa, Chloroxylon, Cistus, Commiphora, Eucalyptus, Guaiacum, Hymenaea, Larix, Liquidambar, Melanorrhoea, Picea, Pinus, Pistacia, Populus, Protium, Schinus, Shorea, Styrax, Trachylobium, Xanthorrhea, &c. Tar, turpentine and other products are obtained by distillation or other treatment of some of these bodies, chiefly the resins of the Coniferae.

Dye-stuffs. Many vegetable dyes are now superseded by artificial products, *e.g.* madder by alizarin. In some cases the colouring matter exists in the plant as such, in others it is prepared by oxidation or otherwise. Among the most important plants yielding dyes are Alkanna, Bixa, Caesalpinia, Carthamus (rouge), Chlorophora (fustic), Cladrastis, Crocus (saffron), Crozophora, Curcuma (turmeric), Garcinia (gamboge), Haematoxylon (logwood), Indigofera (indigo), Isatis (woad), Lawsonia, Maclura (fustic), Nopalea (used for cochineal-insects), Peganum, Polygonum, Reseda, Rhamnus, Rhus, Rubia (madder), &c.

Oils, Perfumes, &c. We have seen that the non-nitrogenous reserves in seeds are frequently oils, and such oily seeds are largely used as sources of oil; the oil is obtained by pressure. Oil also occurs in some fruits and in other parts of plants. Ethereal oils (volatile) occur in flowers and leaves, &c., often giving characteristic perfumes to the plants containing them; they are generally obtained by distillation.

Fixed oils. The chief sources of these are Aleurites, Arachis, Argania, Barringtonia, Brassica (rape, colza), Cocos, Corylus, Elaeis, Guizotia, Gossypium, Linum, Olea (olive-oil), Ricinus (castor-oil), Schleichera, Sesamum, &c.

Distilled oils. The chief of these are obtained from Andropogon, Calamintha, Cananga, Citrus, Eucalyptus, Jasminum, Lavandula, Lippia, Mentha, Melaleuca, Moringa, Nardostachys, Origanum, Pelargonium, Pogostemon, Reseda, Rosa, Rosmarinus, Santalum, Thymus, Viola, &c.

Firmer fatty bodies, used as butter or grease, are obtained from Bassia, Butyrospermum, Combretum, Pentadesma, &c.

Tanning-stuffs. Tannin is contained in many plants; it often occurs in the cells of growing parts and is then apparently a useful substance in the metabolism. It is often found however as an excretum in bark and elsewhere, and it is such parts that are used as sources of it for commercial purposes. The chief are Acacia, Betula, Butea, Byrsonima, Castanea, Caesalpinia, Gordonia, Pterocarpus, Quercus, Rhus, Rumex, &c.

Miscellaneous useful products. Amongst these may be mentioned *poisons* (Acokanthera, Aconitum, Antiaris, Erythrophlœum, Physostigma, Strychnos, Toxicodendron, &c.), *insect-powders*, &c. (Chenopodium, Cimicifuga, Chrysanthemum, &c.), *soaps* (Chlorogalum, Quillaja, Saponaria, Sapindus), *vegetable ivory* (Phytelephas and other palms), *wax* (Ceroxylon, &c.), *paper* (Broussonetia, Fatsia, Scaevola, &c.), *canes* (Arundo, Calamus, &c.), *teasels* (Dipsacus), *loofahs* (Luffa), *weights* (Abrus), *beads* (Abrus, &c.), *paper* (Stipa, &c), and many others. See the Index.

Ornamental Plants. A great many plants are now cultivated for the sake of the beauty or scent of their foliage or flowers.

Flowering plants. Space will only permit mention of a few of the chief favourites in European gardens and hot-houses. Horticulturists endeavour by careful crossing, hybridising and selection to 'improve' these flowers, making them produce more flowers or more concentrated inflorescences, or *double* flowers (*i.e.* those in which the stamens are petaloid or transformed into extra petals, as in rose, double hawthorn, &c.), or new colours (see p. 94).

Among the chief of these are Abutilon, Acacia,

Aconitum, Althaea (hollyhock), Amaryllis, Anemone, Anthurium, Aquilegia (columbine), Azalea, Begonia, Borago, Cactaceae, Calceolaria, Callistephus (aster), Camellia, Campanula, Cattleya, Ceanothus, Centaurea, Chrysanthemum, Clarkia, Clematis, Colchicum, Collinsia, Convallaria, Correa, Crassula, Crataegus, Crocus, Cyclamen, Cytisus, Dahlia, Daphne, Delphinium (larkspur), Dendrobium, Dianthus, Diervilla, Echeveria, Epacris, Epidendrum, Eranthis, Erica (heath), Eryngium, Euphorbia, Freesia, Fuchsia, Galanthus (snowdrop), Gardenia, Gentiana, Gladiolus, Helianthus (sunflower), Helleborus, Hoya, Hyacinthus, Hydrangea, Hypericum, Iberis, Impatiens, Iris, Ixora, Jasminum, Laburnum, Lantana, Lathyrus (sweet-pea), Lavandula, Lilium, Loasa, Lobelia, Lonicera, Lunaria, Lupinus, Lychnis, Matthiola (stock), Medinilla, Mimulus, Mirabilis, Nelumbium, Narcissus, Nemophila, Nigella, Nymphaea, Oenothera, Oncidium, Orchidaceae, Paeonia, Papaver (poppy), Passiflora, Pelargonium, Pentstemon, Petunia, Philadelphus, Phlox, Potentilla, Primula, Ranunculus, Reseda (mignonette), Rhododendron, Ribes, Rosa, Salvia, Saxifraga, Senecio, Sinningia (Gloxinia), Solanum, Solidago, Spiraea, Stephanotis, Syringa (lilac), Thunbergia, Thymus, Tropaeolum, Tulipa, Verbascum, Verbena, Veronica, Viola, Wistaria, Zinnia.

Foliage-plants. Many herbs are cultivated for the sake of their coloured or variegated foliage, *e.g.* Coleus, Caladium, Croton, Beta, Phalaris, &c. Others are grown for the handsomeness or for the size or evergreen nature of their leaves, *e.g.* many Palms, Musa, Pandanus, Cycads, Ferns, Selaginellas, &c., in hot-houses, and laurels (Prunus), Gunnera, Coniferae, &c., out-of-doors. Trees also are frequently planted for ornamental purposes; besides the ordinary Conifers, oaks, beeches, elms, birches, ashes, &c. of Europe, many others are used, *e.g.* Aesculus, Ailanthus, Acer, Liriodendron, Paulownia, Robinia, &c.

The student should consult other works dealing with the subjects of this chapter, *e.g.* Fream's *Elements of Agriculture,* Nicholls' *Tropical Agriculture,* Lindley's *Theory and Practice of Horticulture,* Wiesner's *Rohstoffe des Pflanzenreichs,* F. von Mueller's *Select Extratropical Plants,* the *Treasury of Botany,* the *Guides* to Kew Gardens, Smith's *Dictionary of Economic Botany,* Haldane's *Subtropical Cultivations and Climates* &c.

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When two or more pages are mentioned, the first is that upon which the term or subject in question is more particularly defined or described.

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